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SOCIAL ORGANIZATION AND SOCIAL STATUS IN RELATION TO ASPECTS OF ACTIVITY IN RICHARDSON'S GROUND SQUIRREL, *SPERMOPHILUS RICHARDSONII*

by

© SUSAN WEHRELL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Social Organization and Social Status in Relation to Aspects of Activity in Richardson's Ground Squirrel, *Spermophilus richardsonii*" submitted by Susan Wehrell in partial fulfilment of the requirements for the degree of Master of Science.

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ABSTRACT

The object of this behavior study was twofold: to determine the social organization within a colony of Richardson's ground squirrels and to determine any relationships between different aspects of activity and social status of the individuals. Ground squirrels were live-trapped and dye-marked for field identification. All individuals were observed five days a week from 8:00 to noon and from 2:00 to 6:00 p.m., M.D.T., the periods of greatest above ground activity. Activity was recorded at five minute intervals and all components of interactions between two ground squirrels were noted.

Female ground squirrels in this parkland ecotone occupied nearly exclusive spatial territories although trespassing by individuals occurred. Territorial boundaries were most distinct when young animals were born and living underground. Territories in this colony were arranged spatially in a series of concentric rings. There is some evidence for a hierarchy superimposed on a territorial system of social organization in that females in the center are dominant over their more peripheral neighbors in some circumstances. There is also a tendency among female ground squirrels to actively seek a central position within the colony.

There were more interactions between neighboring animals than non-neighbors. Chasing was the most frequent type of interaction between non-neighbors but both attacking and threatening only were more frequent between neighbors. The most severe components of interactions, attacking and fighting, were most common during those parts of the season when territorial boundaries were least distinct. Both the severity and frequency of interactions decreased prior to the onset of torpor.

Data for eleven types of activity were compared for central and peripheral females. There were no significant differences between the two groups for any non-social activity (feeding, food gathering, digging, bedding material collection, grooming and sunning). The social activities considered were alert behavior, investigating, visiting burrows, marking, and interacting. Differences between groups for two types of social activity were significant. The occurrence of both marking and interacting was higher for central than for peripheral females.

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INTRODUCTION

The purpose of this behavior study was to determine possible relationships between different aspects of activity and social status within a group of ground-dwelling sciurid rodents, *Spermophilus richardsonii richardsonii* (Sabine). This species of ground squirrel is particularly suited to a field study of this type, since it is completely diurnal and all above ground activity occurs between April and August; this period is delineated by the emergence from and subsequent re-entrance into a period of torpor.

There is little precedent for a study of this type. Studies of individual aspects of activity are frequently confined to a laboratory situation. In many laboratory studies, animal "activity" has been grossly subdivided into two categories: "motor" activity, measured by revolutions in a running wheel, and "exploratory" behavior, measured by the number of squares crossed on an open field board (McClearn, 1959 and 1960; Thompson, 1956; Wimer and Stearns, 1964). Southwick and Clark (1968) found different correlations between "aggressive" scores and open field behavior for two strains of mice, and Lagerspetz (1961) found a slight correlation between aggressiveness and both categories of activity among individuals of one strain of mouse.

When activity is further subdivided into components such as feeding, grooming, etc., the tendency among investigators has been to tabulate the activities of a single animal throughout a given time interval (Wiens, 1969), or to simply describe an activity based on a composite of group observations (Balph and Stokes, 1963; Clark and Denniston, 1970). "Activity" in field studies on ground squirrels has been used to refer to the

presence or absence of animals above ground at different times of the day or during different times of the year (Bradley, 1967; Clark, 1970; Shaw, 1945). Seasonal variations in various components of activity have been documented by Yeaton (1969) for different sex and age classes in *S. richardsonii*. My study considers a variety of activities common to all members of a colony of ground squirrels with the aim of comparing individual differences in the frequency or duration of these activities.

Relating aspects of activity to social status for *S. richardsonii* is complicated by the absence of adequate information on the social organization of the species. Studies on other species of ground squirrels have indicated a variety of social organizations within the genus *Spermophilus*. A linear hierarchy has been described for the golden-mantled ground squirrel (*S. lateralis*) in laboratory experiments (Grubitz, 1968), while Wirtz (1967) suggested a grouped social order (one dominant and equal-rank subordinates) for the same species under an artificial situation in the field. Balph and Stokes (1963) reported a linear rank order among neighboring males of a *S. armatus* colony and Turner et. al. (1970) have recorded the same type of social organization for *S. tridecemlineatus*. Quanstrom (1968) described a group social hierarchy for female *S. richardsonii* composed of one dominant female with subordinate and "outcast" females in the colony. He mentions little about organization among males or the social relationships between males and females. In addition, the type of social organization described as "typical" for a species may vary seasonally; a system that is manifest during the breeding season of a species may be modified or absent during the rest of the year.

Due to the aforementioned complications, the purpose of this study is twofold, and the achievement of the second objective is dependent upon

completion of the first:

1. to determine the type of social organization within a colony of Richardson's ground squirrels throughout the season of above ground activity and the relative rank of the animals independent of any territorial influence.

2. to record the frequency and duration of different types of activity for each animal in the group and determine any consistent relationship between aspects of activity and social status.

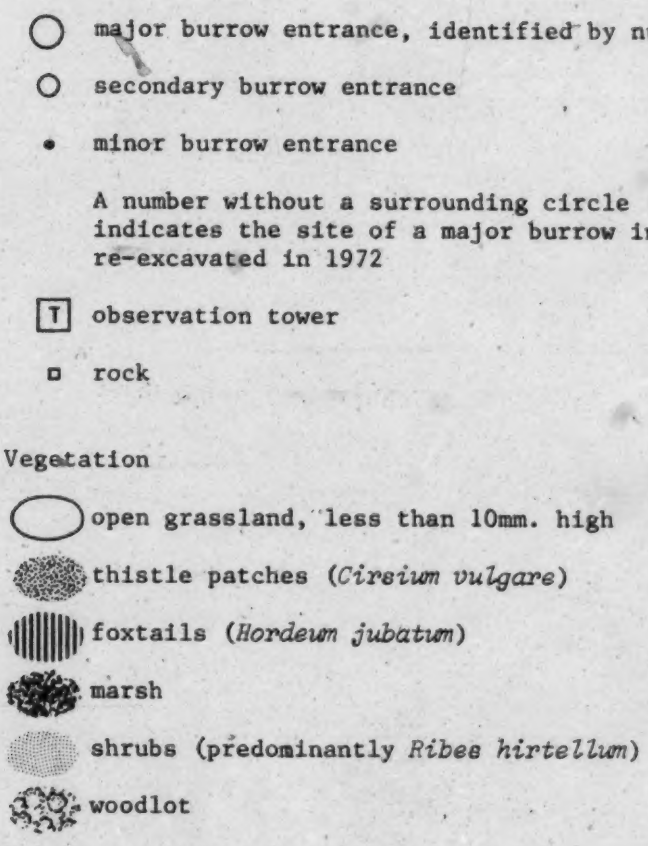
THE STUDY AREA

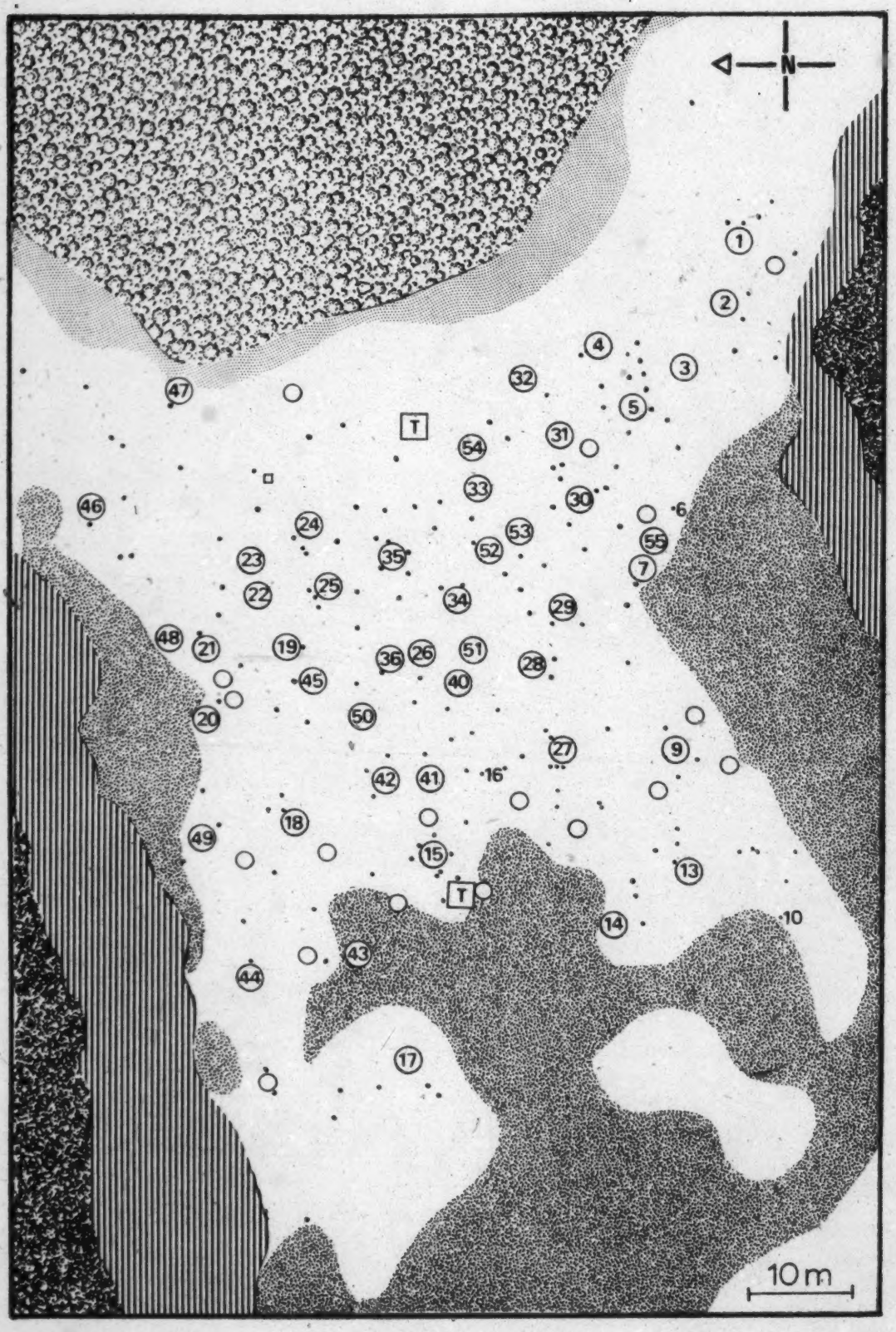
The field work was done on the northern side of Ministik Lake (Lat. 53°22', Long. 112°59'), 38.3 kilometers (23 miles) southeast of Edmonton, Alberta. The 0.72 hectare (1.78 acres) comprising the study area is part of a larger area maintained as a waterfowl refuge for the past 30 years. Public access is limited and there have been no recent attempts to alter the ground squirrel population by removal trapping or poisoning.

The area of mixed grassland-woodland is typical of the aspen parkland ecotone described by Moss (1955). The ground squirrel colony was located on 0.40 hectares (0.99 acres) of open grassland in the center of the study area (Figure 1). The open area was bordered on two sides by woodlots and on the third side by a marsh. The fourth side was bounded by large patches of thistles (*Cirsium vulgare*). These three types of barriers provided natural limits to the open areas utilized by the ground squirrels and also decreased access to ground squirrels outside the area.

The woodlot canopy was formed by aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and willows (*Salix discolor*) along with a very few white spruce (*Picea glauca*) and black spruce (*P. mariana*). The major shrub surrounding the woodlot was wild gooseberry (*Ribes hirtellum*). Dandelion (*Taraxacum ceratophorum* and *T. officinale*) and pussy-toes (*Antennaria nitida*) extended from the edges of the woodlot into the open grassy areas. The major grasses on the study area were *Poa pratensis* and *P. nervosa*. The grass was kept short by a herd of cattle which was pastured in the area from mid-May to the end of September. Between the marsh and the study area were large patches of foxtails (*Hordeum jubatum*). Marsh

Figure 1: Map of study area near Ministik Lake (Lat. 53° 22', Long. 112° 59').

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vegetation was predominantly reed grass (*Calamagrostis canadensis*).

Predation on the ground squirrels was attempted by long-tailed weasels (*Mustela frenata*), coyotes (*Canis latrans*), and red-tailed hawks (*Buteo jamaicensis*) while the study was in progress. Other potential predators on the population were short-tailed weasels (*Mustela erminea*) and other species of large hawks.

Three types of ground squirrel burrow entrances were found on the study area. The most readily noticeable are those surrounded by a large mound of dirt one to two meters in diameter. Re-excavation of a burrow system by the occupant in spring and continued maintenance of open passageways results in continuous additions of dirt to the mound throughout the season. After all adults have begun torpor the mounds are often overgrown with thistles and grasses. Burrow entrances surrounded by large dirt mounds will hereafter be referred to as major burrow entrances.

Surrounding a major burrow entrance are many small holes seldom greater than six centimeters (2.5 inches) in diameter. These are almost always connected with the major burrow entrance and are not surrounded by dirt mounds. All the dirt removed in excavating these "back doors" is hauled back to the major burrow entrance and deposited on the dirt mound. Grass immediately over the hole is cut and pulled back into the hole. The number and location of these small holes changes over the season and occasionally one of these may be enlarged to form a major or secondary burrow entrance. These "back doors" are more properly called minor burrow entrances. Major and minor burrow entrances together comprise a major burrow system.

Occasionally a burrow entrance will be excavated and dirt deposited around outside but the dirt pile never reaches the proportions described

for major burrow entrances; the pile diameter may be one-half meter or less and there are seldom more than a few minor burrow entrances connected to it. These secondary burrows are most frequently found near the periphery of an animal's defended area. Secondary and minor burrow entrances together comprise a secondary burrow system.

A fourth type of burrow entrance was found around the periphery of the open area and in the woodlots and thistle patches. The hole, like the minor burrow entrances, was seldom more than six centimeters in diameter, but there was frequently a small amount of dirt scattered around the entrance. There were no minor burrow entrances associated with these peripheral burrows and the tunnel usually ended blindly within a meter. These peripheral burrows were never observed to be defended and provided only temporary shelter from a predator or from the aggressive advances of another ground squirrel.

MATERIALS AND METHODS

Preliminary behavioral observations were made in 1971 and all animals present that season, including almost all juveniles, were marked for identification the following year. Records for 1971 were incomplete and only the data for the 1972 season were utilized in statistical tests.

In 1972, all animals were live-trapped for the first time within two weeks of emergence from winter hibernation. Traps were made from a coil of copper wire similar to those described by Prychodko (1952) and modified by A. L. Steiner to include a one-way door at each end of the coil (Figure 2). The traps could be bent and were placed just inside a burrow entrance, providing a successful and highly selective method of trapping. The animals could be tagged and dyed while in the trap without direct handling.

Adults were ear-tagged with #1 fingerling ear tags and juveniles were toe clipped for positive identification. For field observation, each adult was given an individual dye mark, using Miss Clairol velvet black (#51S) commercial hair coloring for female ground squirrels and Miss Clairol flame (#33S) for males (Figure 3). Animals were held in the trap for about an hour until the dye mark was dry and were released into a plastic bag and weighed before being released at their capture site. Animals were re-trapped and redyed whenever the identifying mark became too faded to see from a distance; usually redying was necessary every month and a half to two months. Observations on activity were not recorded on days when re-trapping and redying was in progress.

Observations were made from two six-foot towers at either side of the study area. Blinds were not used and were not necessary. After the

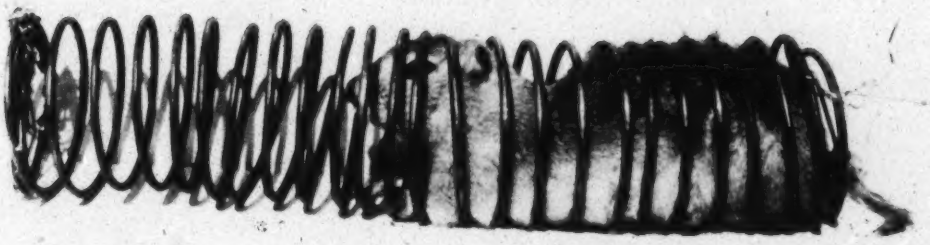


Figure 2: Female Richardson's ground squirrel in coil trap. One-way doors at both ends of the trap were wired shut to prevent accidental release of the animal.

Figure 3: Female Richardson's ground squirrel with black dye mark on shoulder. Dye marks were identical on both sides of the animal's body.

first few days, the squirrels ignored the presence of observers on the towers and eventually even the movement of observers through the colony at the beginning and end of each observation period did not cause any major alteration in the squirrels' activity. There was no noticeable avoidance of the towers by the squirrels and the only direct effect on the animals' behavior was observed infrequently on very hot afternoons when the squirrel closest to tower two would lie in the shade of the tower platform for brief intervals.

Observations of the population were made for four or five consecutive days every week, weather permitting, from mid-April until the end of August, 1972. During heavy rains or high winds, the ground squirrels remained underground or came above ground very infrequently and observations were discontinued. Observation days usually ran from Monday through Friday unless inclement weather disrupted the schedule for more than one day, in which case observations were continued on Saturday and Sunday. Daily observations were made with the aid of 7 X 35 binoculars from 8:00 A.M. to noon and 2:00 to 6:00 P.M. Mountain Daylight time. Ground squirrels are unimodal in activity in April [illegible] May are already bimodal on moderate and warm days. The time intervals were chosen on the basis of the first year's field work (1971) to encompass the peaks of activity for most of the season.

The data for 1972 are more complete than records for 1971 since during the second summer I was aided by an assistant and the entire study area could be observed. Each observer covered approximately half of the field with an area of overlap in the center. Comparison of the data recorded for the more central animals showed no major differences in the information recorded by my assistant and myself. We exchanged places each

morning and each afternoon so that both of us were familiar with the entire area and with each individual animal. Alternating positions of observation would also cancel any slight differences between individual observers which might otherwise influence the results of statistical tests.

The activity of each animal was recorded at least once every five minutes and each half of the area was under continuous observation so that changes in each animal's activity would be noticed. The majority of non-social activities (feeding, grooming, digging, etc.) were usually continued longer than five minutes and were recorded only once per interval. Various activities of less than five minutes duration were recorded as fractions of an interval. A few activities (marking, visiting, and investigating) which were completed within a few seconds were recorded by frequency only. For statistical analyses, each occurrence of these activities was considered to be one minute in duration. The movements and postural components of interactions between two animals were recorded in their entirety. Numbered stakes were used to indicate the major burrow systems on the area and the location of the animals at each interval was estimated and recorded with respect to these stakes and other prominent landmarks.

In addition, notes were made every one and one half hours estimating degree of overcast or cloudiness and wind velocity, the latter using a Beaufort wind scale. Temperature was recorded near the beginning and end of each of the two daily observation periods. Temperature readings were taken in the shade of one observation tower platform approximately six feet above ground level.

Most of the data used for statistical comparisons was analyzed using a chi-square test for goodness of fit and chi-square 2 X 2 test of

independence. Where other tests have been used, the test value as well as the probability value are given in parentheses. The letter preceding the test value indicates the test used. Tests used and their abbreviations include Student's t-test (t), G-statistic (G), sign test for the paired case (Z), coefficient of correlation (r), and Mann-Whitney U-test (U; for large sample sizes, the value T is given). Probability levels without accompanying test values indicate the use of a chi-square test. In all statistical tests, $p<.10$ was considered slightly significant and values of $p<.05$ were considered significant. Formulas for each test may be found in Sokal and Rohlf (1959).

THE POPULATION

In 1971 there were 13 ground squirrels on the study area; one male, 11 females, and one animal which did not raise a litter but resisted all attempts to capture it. Additional trapping of the entire pasture area gave a total of four males and 22 females, an overall ratio of one male: 5.5 females. Forty-seven young survived long enough to come above ground and were the offspring of nine of the 11 females on the study area. Eight of the 11 females overwintered successfully and seven re-established themselves on the area in 1972. No adult males from 1971 were trapped in 1972 and of six juvenile males established on the area in late August, only one was re-trapped in 1972. Of the 15 juvenile females who did not disperse in 1971 but defended portions of the study area, seven survived the winter and the mothers of at least six of the surviving juvenile females themselves overwintered successfully so that a number of female-young pairs were present in 1972.

In 1972, the population of the study area increased, as did the total number on the entire pasture. Total population of adults in the pasture was two males and 36 females (one male: 18 females). The population on the study area in 1972 consisted of one male and 17 females two weeks after emergence from hibernation. One female disappeared within a few days after it was first trapped and two females were taken by a weasel on June 14. Aside from these losses, the adult population remained constant until early July, when some animals disappeared underground to commence annual episodes of torpidity. Of the 16 females whose activity provided the majority of the data recorded, seven were adults that had lived on the study area in 1971, seven were yearlings born on the study

area in 1971, and two females were unmarked, indicating that they moved onto the area either after the last week in August, 1971, or shortly after emerging from hibernation in 1972. It is likely that the two previously unmarked animals were yearlings since a higher percentage of juvenile females than adult females disperse from a settled area (D. Michener, 1972). Although weight at emergence from hibernation can be used as an estimate of age for some species of ground squirrel (A. L. Steiner, pers. comm.), there is no consistent difference between weights of female adult and yearling Richardson's ground squirrels. Other methods suggested for aging ground squirrels require sacrificing animals (Karpukhin and Karpukhina, 1971; Montgomery et. al., 1971) and are incompatible with a behavior study.

Fifty-five young survived to come above ground and were the offspring of 11 of the 16 females on the study area. Young ground squirrels remain underground for three to four weeks after birth and undoubtedly some young do not survive this period (one female transferred nine live offspring to another nest a few days after birth; three weeks later, however, only five were observed above ground and trapped). Judging from external appearances, almost all females appeared to be pregnant, but five of the 16 did not show signs of lactation. Of the 11 females with litters, five were adults, five were yearlings, and one was of unknown age class.

The one male was a yearling who moved onto the study area from elsewhere as a juvenile in 1971. Adult males became torpid by the first week in July in 1971; in 1972 the only male was last seen on June 5 and then disappeared. In 1972, some females without litters became torpid the last week in June and all were gone by July 6. Some lactating females began torpor on July 14 and the last two were gone by July 29.

Individual animals are designated in the text by single capital letters. Where appropriate, additional information is given by letters in parentheses following the individual letter designation. The first letter in parentheses refers to the animal's age class: adult (A), yearling (Y), or age class unknown (U). The second letter indicates whether a female raised a litter (L) or not (X) during the season. The number following the letters indicates ring location within the colony (1, 2, or 3) and its significance will be explained later.

RESULTS

PART I: SOCIAL ORGANIZATION

Behavioral Components of Interactions

To determine the social organization of the population, the interactions between individuals as well as the location of these interactions were analyzed. An interaction may be broadly defined as any visible behavior of one animal which has a direct, prompt, and observable effect on the behavior of another. When two ground squirrels were in close proximity, one or more of the following behavioral components usually occurred (after Sheppard and Yoshida, 1971):

1. Recognitive contact:

Nose-to-nose: Both animals approach with tails extended horizontally and touch noses. This is often followed by "kissing", nose-to-nose with one or both animal's mouth open.

Nose-to-body: Sometimes follows nose-to-nose contact. One animal touches the body of another with its nose.

Nose-to-anus: One or both animals touch the tail or anal region of the other.

All three types of recognitive contact are frequent between adult females and their young and between young siblings. This type of behavior is infrequent between adults and agonistic behavior usually follows this initial contact.

2. Avoidance:

Active avoidance: At the approach or appearance above ground of one animal, another animal stops a given activity and moves away from the

first animal without any actual contact between the two.

Retreat down a burrow: At the approach of an animal, another may cease activity and retreat down a burrow at the approach of the first. This behavior was common among peripheral females at the approach of the male.

3. Agonistic:

Threat: This is usually displayed first by a stationary animal towards an approaching animal; threatening may also be reciprocal. The back is arched, the tail angled upwards and bristled, and the rear end is directed towards the approaching animal. On animals close to the observation towers it was noticed that the anal papillae are frequently extruded in this posture, and defecation of a single pellet was observed once. This posture may be accompanied by sharp frequent calls.

Challenge (called "arching" by Sheppard and Yoshida, 1971): This is similar to the threat posture but the side of the body is presented and the animal frequently advances broadside towards the approaching animal. This posture, too, is frequently accompanied by sharp calls.

Attack: One animal leaps at or on the other.

Fight: The animals roll over and over together, striking with both feet and teeth.

Chase: A chase may follow any one of the aforementioned behavioral components. A chase is initiated in one of two ways: one animal runs towards another who flees at the approach of the first animal, or one animal already in motion is pursued by another. The length of chase varies from a few feet to the length of the entire study area. A chase may be followed by other agonistic components if the chaser overtakes the chasee.

4. Cohesive:

Allo-grooming: One animal grooms the fur of another, using teeth or forepaws.

Mutual grooming: Two animals groom each other, alternately or at the same time.

Seasonal Intervals

It is reasonable to assume that seasonal physiological changes characteristic of Richardson's ground squirrels as a species might also influence the behavior of the animals. Since combining activity frequencies and durations for the entire study period might obscure seasonal or individual differences, the season's data were divided into the following intervals for analysis:

I. April 17 to May 7: This period of settling in began with the animals' emergence from hibernation. Old burrow systems were re-excavated and new burrow systems added. This interval included the beginning of territory establishment and agonistic encounters between individuals were frequent.

II. May 8 to May 30: Young were born and remained underground; the majority of litters were born in the first week of this period. Defense of burrow systems and establishment of boundaries between neighboring territories was more prevalent during this interval than any other.

III. June 1 to June 14: Young animals appeared above ground. Juveniles first emerged on May 29 and almost all juveniles had been trapped and toe-clipped by June 1. During this interval young animals spent progressively more time above ground and adult females tended to spend more time away from the immediate nest burrow vicinity. The male disappeared

during this period.

IV. June 15 to June 30: This interval was characterized by changes in the spatial location of some animals and dispersal of the young. Two adult females were taken by a weasel from the eastern end of the study area on the afternoon of June 14, resulting in the re-organization of defended areas in that portion of the study area and the appropriation of portions of the vacant area by a more peripheral adult female. There was a noticeable decrease in the number of young on the study area in the last week in June. This interval also included preparation for torpor among females that did not raise litters. If the loss of the two adults had not occurred, this interval would have been combined with interval III.

V. July 1 to July 31: Young continued to disappear from the study area but at a much slower rate. Lactating females prepared for torpor. Non-lactating females had all become torpid by July 4, and all lactating females entered torpor by July 31. The social organization during each of these intervals will be analyzed and described.

Social Organization during Interval I, April 17 to May 7

1. Emergence and settling in. Before regular observations began on April 17, sporadic observations were made while trapping the animals for the first time in 1972 and during other short periods when the weather permitted. On March 26, the first two animals on the study area, both females, emerged from hibernation. On March 31 there was one more animal and by April 9 there were at least 10 animals, including the one male. During the following week, most of the study area remained snow covered and received a few more inches of new snow. Several animals fed within a meter of each other on the few exposed areas. Little agonistic

behavior was seen at this time. By April 17, the snow was gone from the grassland areas entirely, and the number of interactions increased to the highest frequency of the entire season (Figure 4).

Twelve of the original 18 animals had hibernated around the periphery of the open area and six emerged from more central areas. Three of the peripheral animals moved towards the center and established themselves in areas between the central six animals, although one of the three was displaced at the beginning of interval II and resumed a peripheral position (Figure 5).

The three peripheral animals which attempted to relocate in a more central position on the open area followed a consistent sequence in response to attack from surrounding central animals. The challenger would make repeated trips to investigate a particular burrow system and would be consistently attacked and chased away. After a few days of running from attacks and threats, the challenger would avoid conflict by retreating down the burrow. If the challenger was not routed at this point, she would begin to spend progressively more time in the immediate vicinity of the burrow and the frequency of attacks by neighboring animals decreased. Upon being threatened on the mound surrounding the burrow opening, the challenger would return the threat or engage in a fight rather than retreat. The final step in acquiring a burrow occurred when the challenger began to initiate chases and attack trespassers on the burrow hill, eventually establishing tentative borderlines between the area surrounding the burrow and the burrow systems of the next closest animals. The entire process occupied about a week.

Beginning on April 17, females F and D frequently wandered into areas more central than their hibernation sites and were repeatedly chased

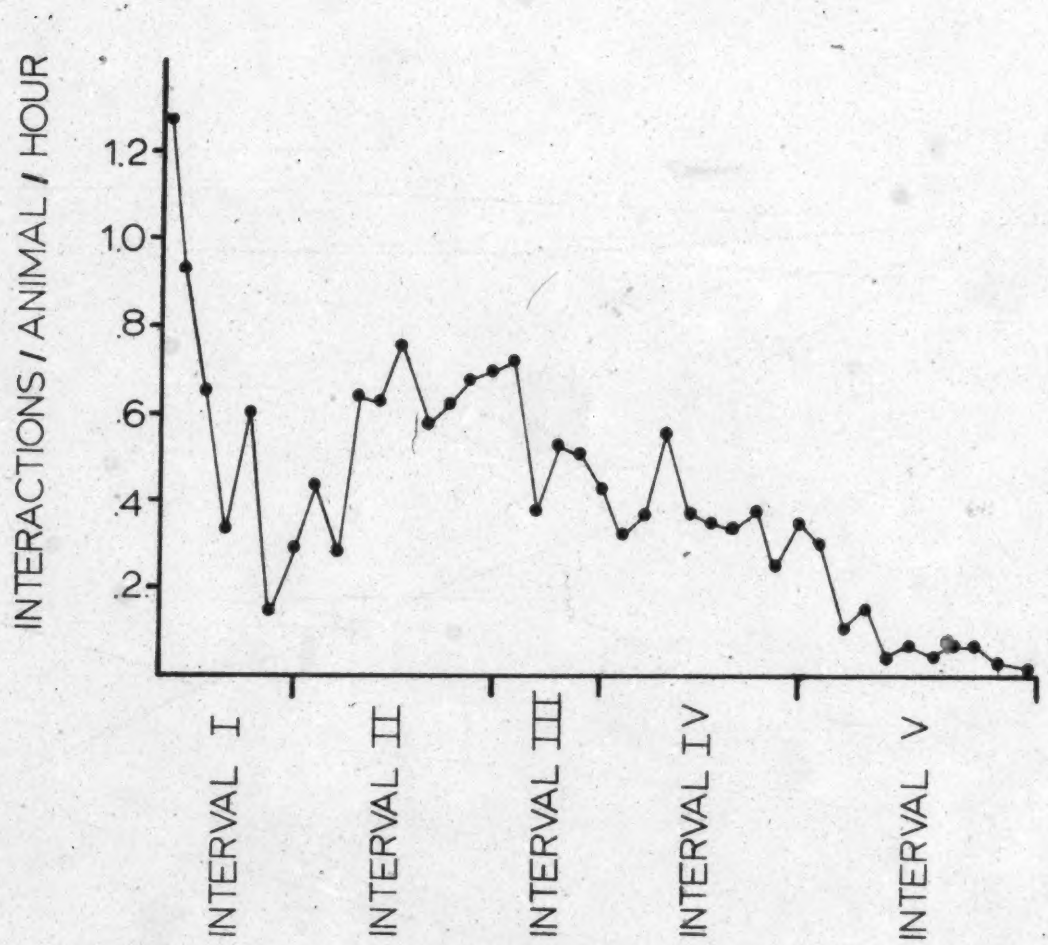


Figure 4: Frequency of interactions between adult Richardson ground squirrels for the entire season of above ground activity. Frequencies were calculated only on days with favorable weather and for observation periods longer than three hours.

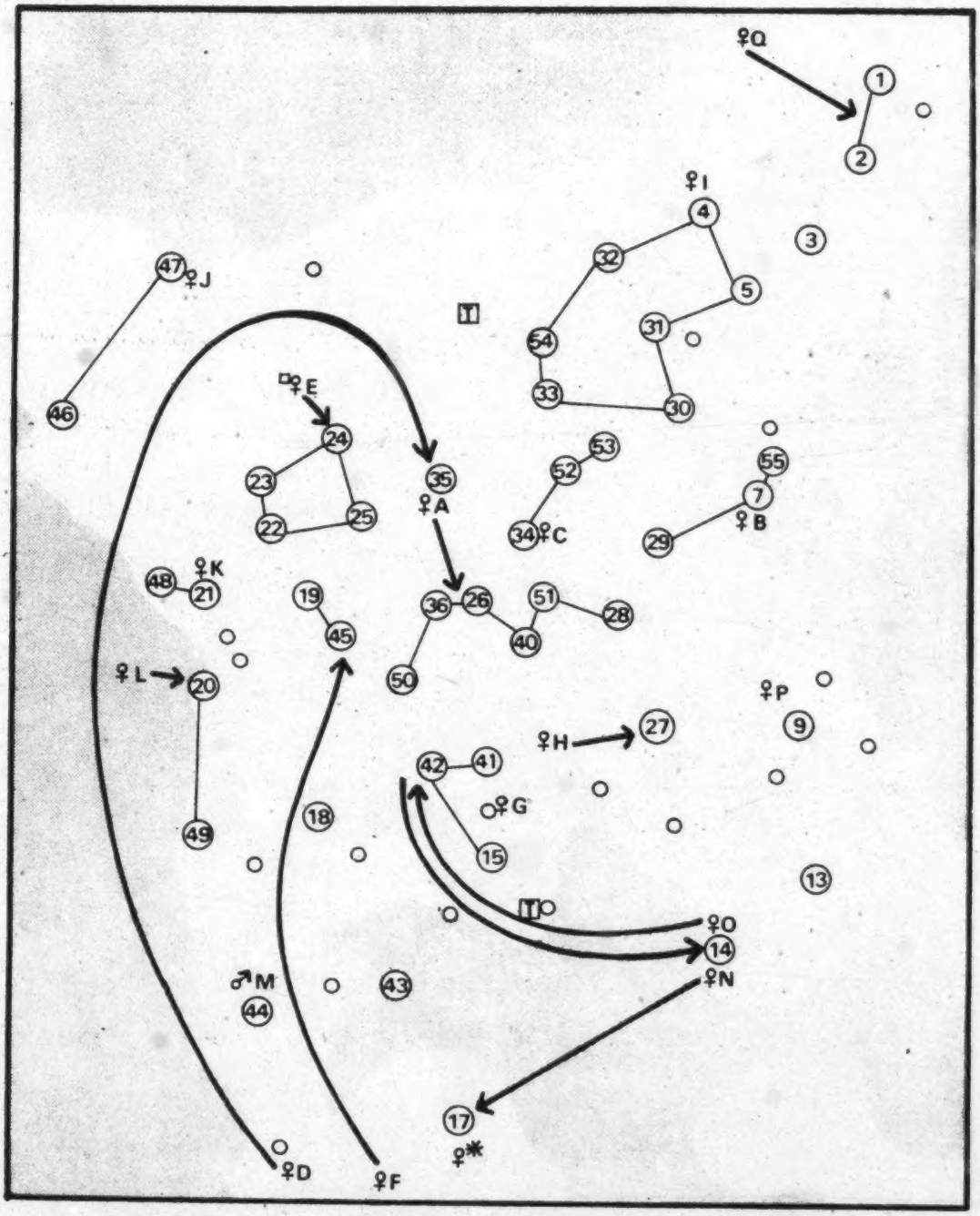


Figure 5: Overwinter location and subsequent movements of individuals during interval I, April 17 to May 7. The position of the individual symbols indicates overwinter location.

→ = movement after emergence

○-○ = burrow systems actively defended by animal

* = disappeared shortly after emergence

away. On April 19, female D began to retreat underground at burrow #35 when threatened or attacked by surrounding females and on April 21 was observed to chase female E away from burrow #35; she continued to exclude other trespassers from the area for the entire season. Female F took longer to become established at burrow #19 and it wasn't until April 21 that she retreated down the burrow at 19 rather than being chased away by the surrounding animals. Not until April 27 did she successfully exclude other ground squirrels from the immediate area around #19.

Female O who attempted to move from burrow #14 to #42 followed the initial part of the settling in pattern in that she eventually took refuge down burrow #42 rather than being chased away. But she was always unsuccessful when she attempted to chase another animal away from the burrow entrance. Eventually, she herself was repeatedly chased away from #42 by other animals and when threatened her response was to flee rather than retreat down the burrow. By the end of interval one, she was spending most of her time around burrow #14 which was more peripheral and was, by that time, unoccupied (female N moved from burrow #14 to #17). Even the presence of her litter which was born at #42 and kept there for a few days did not result in a strong enough site attachment for successful exclusion of conspecifics from the vicinity of burrow #42. Female O finally abandoned #42 on May 8 when she moved five live young to a minor burrow entrance ten feet south of burrow #14, where all juveniles survived to emerge above ground at the end of May.

The process of settling in is further complicated by the predicament of any two animals which emerge from hibernation within a few meters of each other, and the resulting agonistic encounters contribute to the high level of social activity. Since all adult females were dormant by

the beginning of August, juvenile animals which had not dispersed used and defended parts of or entire areas previously occupied by their mothers or other adults. If both adult and yearling hibernating in close proximity survived to the following spring, then agonistic behavior between the two occurred periodically until one animal was displaced.

2. Location of interactions. Although individual animals consistently occupied certain burrow systems, any territorial boundaries between these burrows were not consistent at this time. The term "central area" refers to the area containing the burrow systems of the eight animals (adult females A, F, and H, and yearling females B, C, D, E and G) closest to the center of the study area. The "peripheral area" includes the burrow systems of nine animals (adult females I, K, L, N, yearling females J and O, females of unknown age class P and Q, and the male, M) around the outer edge of the study area.

The majority of interactions occurred in the central part of the study area (Figure 6). There were fewer interactions around the periphery and analysis of the total number of interactions involving central and peripheral females indicated a significantly higher number of interactions for this interval among animals towards the center ($U=58$, $p<.01$).

The central area contained three adult females and five yearling females of which yearling D and adult F had moved in from a more peripheral position. The high number of interactions near the center was certainly due in part to the conflict involved during the settling in of these two animals, but this would not account for the high number of interactions elsewhere around centrally located burrow systems. The total number of interactions recorded for each animal can be subdivided according

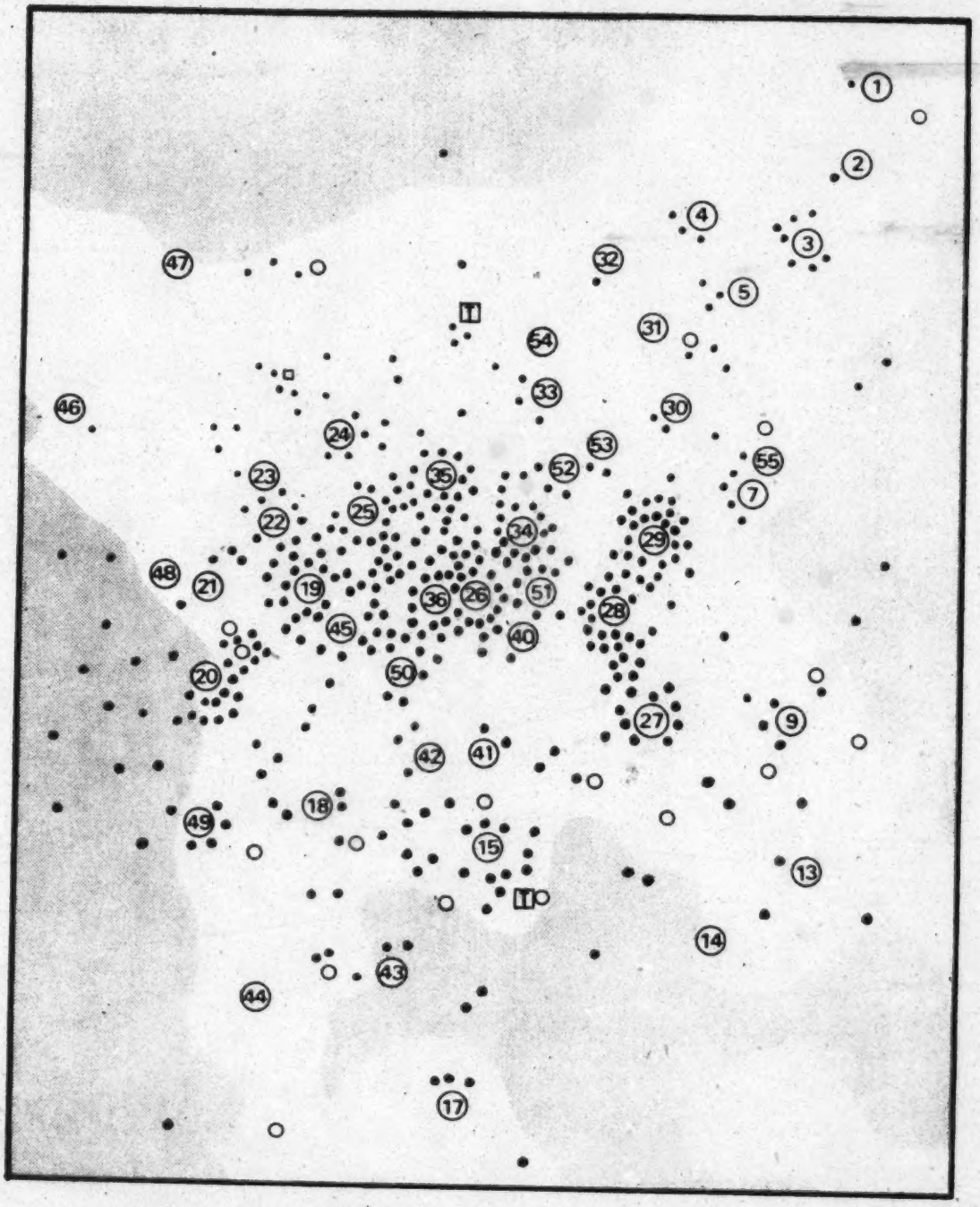


Figure 6: Location of interactions during interval I, April 17 to May 7. Each solid dot represents one interaction between two ground squirrels.

to whether the animal initiated the encounter or whether the animal was involved in an encounter initiated by another ground squirrel. The two newcomers initiated the fewest number of encounters relative to their total score and their involvement rate is the highest among the central animals (Table 1).

An additional factor contributed to the high incidence of interactions towards the center of the study area. Interactions involving the eight more peripherally located females were subdivided according to whether the second animal involved lived in a peripheral or more central position. Seven of the eight peripheral females showed a higher incidence of interaction with central females than with other peripheral females ($Z = 1.77$, $p=.07$).

It appears that female Richardson's ground squirrels actively seek a central location within a colony and the advantages of a central over a peripheral position will be considered later. Evidence supporting this central settlement tendency includes: 1. the attempt of three animals to move from a peripheral hibernation site to more central burrow systems, 2. the majority of interactions occurred in the central area, and 3. peripheral females interacted more with central animals than with other females around the periphery. If there was no central settlement tendency, the locations of interactions should have been more evenly distributed over the area available as each animal sought to establish a territory. The disproportional distribution may indicate that there was more competition for central than peripheral locations. The rules of probability would predict that peripheral females would interact equally with all adjacent animals. That they interact more with animals centripetal to them might indicate more competition for space towards the center than

Table 1: Initiation and involvement rate in interactions of centrally located female ground squirrels during interval I, April 17 to May 7.

	Female	Total Number of Interactions	Initiation Rate [1]	Involvement Rate [1]
Adults	A	56	73.2	26.8
	H	25	64.0	36.0
	* F	54	24.1	75.9
Yearlings	* D	86	37.2	62.8
	B	43	44.2	55.8
	C	82	65.8	34.2
	E	66	81.8	18.2
	G	46	58.7	41.3

[1] Rate expressed as percent of total number of interactions for each animal.

* Animal moved into the central area from a peripheral position.

for space to either side.

3. Components of interactions. Three hundred fifty of the 414 interactions occurring during interval I were subdivided according to the type of agonistic behavior that occurred during each encounter. Interactions in which more than one component of agonistic behavior occurred were classified according to the most severe (i.e. potential for injury) component. Thus an interaction involving a threat and chase would be tabulated under "chasing". Of the 66 interactions that were not included in the analysis, 29 were interactions involving three or more animals and are analyzed later as "compound" encounters; the remaining 35 interactions were not observed in their entirety and records of these encounters are incomplete (Table 2).

Chasing was the most frequent component of agonistic behavior (Table 3). In addition, chases accompanied 28 percent of all attacks and 85 percent of all fights. Attacks comprised nearly a third of all interactions. Interactions involving only threatening or challenging accounted for 13 percent. Fighting was infrequent as were interactions characterized by avoidance only. In almost all instances of avoidance, the trespasser retreated from an area at the approach of the resident; in two instances, the trespasser retreated at the approach of a resident's neighbor.

The terms "resident" and "trespasser" were applied to the two animals involved in an encounter with reference to the location of an interaction. A resident was the animal who had dug or re-excavated a burrow system at a particular location and who attempted to exclude conspecifics from an area around the burrow. A trespasser was the animal that was closer to another animal's burrow system than to its own when the interaction occurred. As the ground squirrel social organization became more clear,

Table 2: Total number of interactions, number of interactions analyzed, number of compound interactions, and hours of observation for each interval, 1972.

	Interval I	II	III	IV	V	Total for season
Total number of interactions for each interval	414	740	325	290	41	1810
Number of compound interactions	29	8	1	0	0	38
Number of interactions analyzed	350	649	283	274	41	1597
Interactions incompletely observed or recorded	35	83	41	16	0	175
Hours of observation per interval	44	79	38	58	114	332

Table 3: Components of interactions for each interval. All figures are given as percent of total number of interactions analyzed (N) for each interval.

Component	Interval I	II	III	IV	V
Avoidance	3.45	2.16	1.42	6.20	12.20
Threatening or Challenging	12.93	15.10	8.83	23.00	36.58
Chasing	50.29	49.61	46.64	40.15	24.39
Attacking	29.31	21.42	29.68	26.64	19.51
Fighting	4.02	11.71	13.43	4.01	7.32
N =	350	649	283	274	41

these terms were modified, and the alteration of these definitions will be presented later.

During interval I, residents initiated 70.97 percent of 348 encounters, while trespassing animals initiated 13.51 percent of interactions against residents (Table 4). The remaining 15.52 percent of total encounters were initiated by individuals at a location from which neighboring animals usually excluded conspecifics. This was not an interaction initiated by a trespasser against the resident, but against a third individual who was also trespassing.

4. Compound interactions. Interval I has been described as a time of "settling in" when individuals become established at a location to the exclusion of other conspecifics. Interactions during this interval involving more than two animals occurred to a greater degree than at any other time during the season. These were termed "compound" interactions to indicate the participation of three or more animals, although no cooperative aggression is implied.

Compound interactions were recorded only once after May 12 and did not occur after June 14. Of a total of 38 compound interactions for the entire season, 29 occurred during interval I, and the highest number per day was recorded during the first few days of observation in mid-April. Only two of the 38 encounters involved the one male in the colony. During the first interval when compound interactions were the most frequent, they only comprised seven percent of the total number of interactions (Table 2, pg. 30).

Table 4: Interactions initiated by residents, trespassers, and residents from an adjacent territory. All figures are given as percent of the total number of interactions (N) for each interval.

Initiated by:	Interval I	II	III	IV	V
Resident	70.57	75.35	78.45	55.11	60.98
Trespasser	14.29	9.55	12.72	12.41	9.76
Resident from adjacent territory	15.14	15.10	8.83	32.48	29.27
Against:					
male	5.14	1.23			
neighbor	4.57	8.63	5.30	10.95	21.95
non-neighbor	5.43	5.24	3.53	21.53	7.32
N =	350	649	283	274	41

5. Interactions between sexes and between age classes. The number of interactions between females of different age classes (i.e. adult and yearling) and between females of different age classes and the one male were tabulated and analyzed statistically using a chi-square test. The number of interactions expected due to the number of animals present in each category was calculated and compared to the observed values. The following results were statistically significant ($p < .05$): Both yearling and adult females interacted with the male much more frequently than expected by chance. During this interval the male wandered over the entire study area and interacted with each female (except one) between one and ten times. He was almost always threatened or challenged by resident females and then chased. Although he was involved in 73 interactions, he initiated only six of them; in four of these six encounters, he chased trespassing females from the vicinity of his own burrow system on the periphery of the study area (#44). There were significantly fewer interactions between adult females and between adult and yearling females, but a greater number than expected among yearling females. The location of the central yearling females corresponds to the location of many of the interactions during interval I. In the peripheral area, there is a significant difference ($p < .05$) between yearling and adult females in the proportion of interactions initiated by individuals of each age class. Yearlings on the periphery initiated few encounters and had a higher rate of involvement in interactions initiated by adult females (Table 5). There was no corresponding difference between age classes among the central animals.

Yeaton (1972) reported that adult females "tolerated their female offspring of the previous year to some extent" and that agonistic interactions

Table 5: Initiation and involvement rate in interactions of central and peripheral ground squirrels during interval I, April 17 to May 7.

		Animal	Total Number of Interactions	Initiation Rate [1]	Involvement Rate [1]
Ring 1 and 2	Adults	A	56	73.2	26.8
		F	54	24.1	75.9
		H	25	64.0	36.0
	Yearlings	B	43	44.2	55.8
		C	82	65.8	34.2
		D	86	37.2	62.8
		E	66	81.8	18.2
		G	46	58.7	41.3
Ring 3	Adults	I	42	73.8	26.2
		K	49	44.9	55.1
		L	38	73.7	26.3
		N	18	55.6	44.4
	Yearlings	J	27	40.7	59.3
		O	10	30.0	70.0
		M	73	8.2	91.8

[1] Rate expressed as percent of total number of interactions for each animal.

between related adult females included significantly less fighting. Since the relationships between six pairs of females on the study area were known from the previous year, similar comparisons were made. There was no difference in either the frequency or severity of interactions between related as opposed to unrelated individuals.

6. Interactions between neighbors and between non-neighbors. By the end of interval I, it appeared that there was a difference in the agonistic reaction of a resident to the trespassing of a neighbor as opposed to trespassing by more distant animals. "Neighbors" for the purpose of this analysis refers to the animals maintaining burrow systems immediately surrounding a resident animal. "Non-neighbors" refers to animals at least one more burrow system distant from a resident.

To test the possibility of a differential response to the trespassing of neighbors and non-neighbors, the distances for all chases were measured and grouped according to whether the animals involved were neighbors or not. The male was considered in a class by himself, although given his position on the periphery he was by definition a neighbor to at least two other females. Chases between the male and the females adjacent to his main burrow system were discounted in this test. A Mann-Whitney U test applied to the lengths of chases gave significant results in two instances. The male was chased over longer distances than were neighbors of any given female ($T=2.49$, $p<.02$).and non-neighbors were chased for greater distances than neighboring animals ($T=4.38$, $p<.001$). The latter difference cannot be attributed solely to the greater distances between the burrows of neighbors and non-neighbors since it has been mentioned that a sizeable percentage of interactions were initiated by an animal

while in a neighbor's territory against a third animal trespassing. Though the interactions in this case were not all chases, they were most frequently directed against the male ($p < .001$). Residents from a neighboring area chased non-neighbors only slightly more than other neighbors ($p < .10$).

Overall, there were more interactions between neighbors than non-neighbors ($p < .001$) and interactions with the male were more frequent than with female non-neighbors ($p < .001$). In the field it appeared that interactions between non-neighbors were more severe, involving more attacking and fighting with greater risk of injury. However, chasing comprised a larger proportion of interactions between non-neighbors than among neighbors ($p < .001$) and there was no difference in the proportion of fighting within the two groups (Table 6). Attacking was more common among neighbors than non-neighbors ($p < .05$), but more interactions involving only threatening or challenging occurred between neighbors than between non-neighbors ($p < .01$). There was no difference in the proportion of avoidance between the two groups.

Table 6: Components of interactions between neighboring female ground squirrels compared to components of interactions between non-neighboring females during interval I, April 17 to May 7. Interactions involving the male were omitted from the analysis.

Component	Interactions between neighbors: Total number	Interactions between neighbors: % of total number		Interactions between non-neighbors: Total number	Interactions between non-neighbors: % of total number
Avoidance	9	3.98	n.s.	2	3.77
Threatening or Challenging	39	17.26	**	1	1.89
Chasing	86	38.05	***	37	69.81
Attacking	81	35.84	*	10	18.87
Fighting	11	4.87	n.s.	3	5.66
N =	226			53	

n.s. $p > .10$
\+ $p < .10$
* $p < .05$
** $p < .01$
*** $p < .001$

Interval II: May 8 to May 30

1. Interaction rate. The frequency of interactions was low during the first week of interval II compared to the rest of the interval (Figure 4, pg. 22). Judging from external appearances of the animals and estimating backward from the date of the juveniles' emergence, it was during this week that most of the young were born. For a few days following parturition, the females spent most of their time underground, emerging only occasionally to feed. By this time all the animals had established territories somewhere on the area in that they consistently excluded all other ground squirrels from an area around a burrow system or systems. No burrow systems were abandoned by a resident and no major shifts in occupied areas occurred again until the last week in June.

2. Colonial organization: the ring structure. The areas occupied by animals centrally located in the study area were smaller than those of peripheral animals ($t=2.43$, $p<.05$) and certain portions around the periphery were never consistently occupied by any one animal. These were not "neutral" areas since the presence of more than one animal in these areas usually resulted in an interaction, but the areas were never consistently defended by any individual. There were none of these inconsistently defended areas in the central portion of the study area. The number of animals in the central and peripheral areas was tested against an average number per unit area which would exist if the population were evenly distributed over the study area. A G-test on the spatial distribution of the animals was highly significant ($G=9.98$, $p<.01$) confirming that the animals were not distributed evenly over the entire open area; there were significantly more animals than expected in the central

area and fewer around the periphery.

The distribution of the defended areas resembled a series of concentric rings. The rings were slightly irregular in shape due to interruption of the open area by patches of thistles and the woodlot. One adult female occupied the most central location, and the area from which she excluded conspecifics was designated ring 1. The territories of two adult females and five yearling females immediately adjacent to this area were designated ring 2. The remaining peripheral areas at least one territory removed from center were designated ring 3. This last ring contained four adult females, two yearling females, two females of unknown age class, and the one male.

An adjacent animal in a more central position is hereafter referred to as a neighbor "ahead", an adjacent animal in a more peripheral position the neighbor "behind" and adjacent animals in the same ring become neighbors to the side. In ring 2, the general pattern of surrounding areas was one animal ahead, one neighbor to either side and usually two animals behind. The ring 3 animals usually had one neighbor on either side but defended areas such that the more central boundary of the area was established with two ring 2 animals.

3. Influence of spatial location on the outcome of agonistic interactions. The spatial location of an interaction had a major influence on the outcome of an interaction between neighbors. It was evident that more area than the immediate burrow entrance was being defended and consistent boundaries were apparent between neighboring areas. These were established by both animals involved but were not inviolate. One animal approaching the imaginary line might be met by the threatening or

challenging posture of her neighbor. Crossing the "line" usually resulted in more severe agonistic behavior on the part of the resident and an attack or chase (or both) usually ensued. Repeated chases towards and away from an animal's burrow system were frequent and the role of chaser or chasee oscillated with the direction of the chase, with the animal closest to her own burrow system most often the chaser and the trespasser the chasee. The boundaries were not observed to be actively marked by the animals as has been described for some lagomorphs (Mykytowycz, 1962). A few of the boundaries were very consistent in time and space, but the majority shifted a few feet throughout the interval. The best estimate of territories for each animal is illustrated in Figure 7.

Spatial location appears to have a major effect on social interactions but a cause and effect relationship is not implied. Seventy-five percent of all interactions in this interval were initiated by the resident animal and only 9.55 percent by the trespasser (Table 4, pg.33). The remaining interactions (15.10 percent) were initiated against an animal trespassing in a neighboring area, i.e. a resident animal would move into a neighbor's area to exclude a trespassing animal. This type of defense was used more often against other neighbors than non-neighbors ($p<.001$), and occurred slightly more often against the male than against non-neighbors ($p<.10$). The initiator of an interaction was usually, but not always successful in displacing the other animal.

4. Components of interactions. Chasing was the most frequent type of interaction among all animals comprising half the total number of interactions (Table 3, pg. 31). In an additional 7.70 percent a chase was preceded by an attack and in another 10.48 percent chases were followed

Figure 7: Territorial boundaries of Richardson's ground squirrels as determined by interactions between neighboring animals. Letters indicate the resident animals.

Boundary lines

——— (solid line): boundary determined by interactions between neighboring animals. A line running through a burrow entrance indicates that that burrow system was defended alternately by both animals during the season.

- - - - (dashed line): best estimate of boundaries based on low number of interactions between neighbors. For outermost peripheral boundaries, estimate is based on interactions between non-neighbors as well as neighbors.

Thickness of boundary lines indicates the number of interactions between neighbors used to determine the boundary.

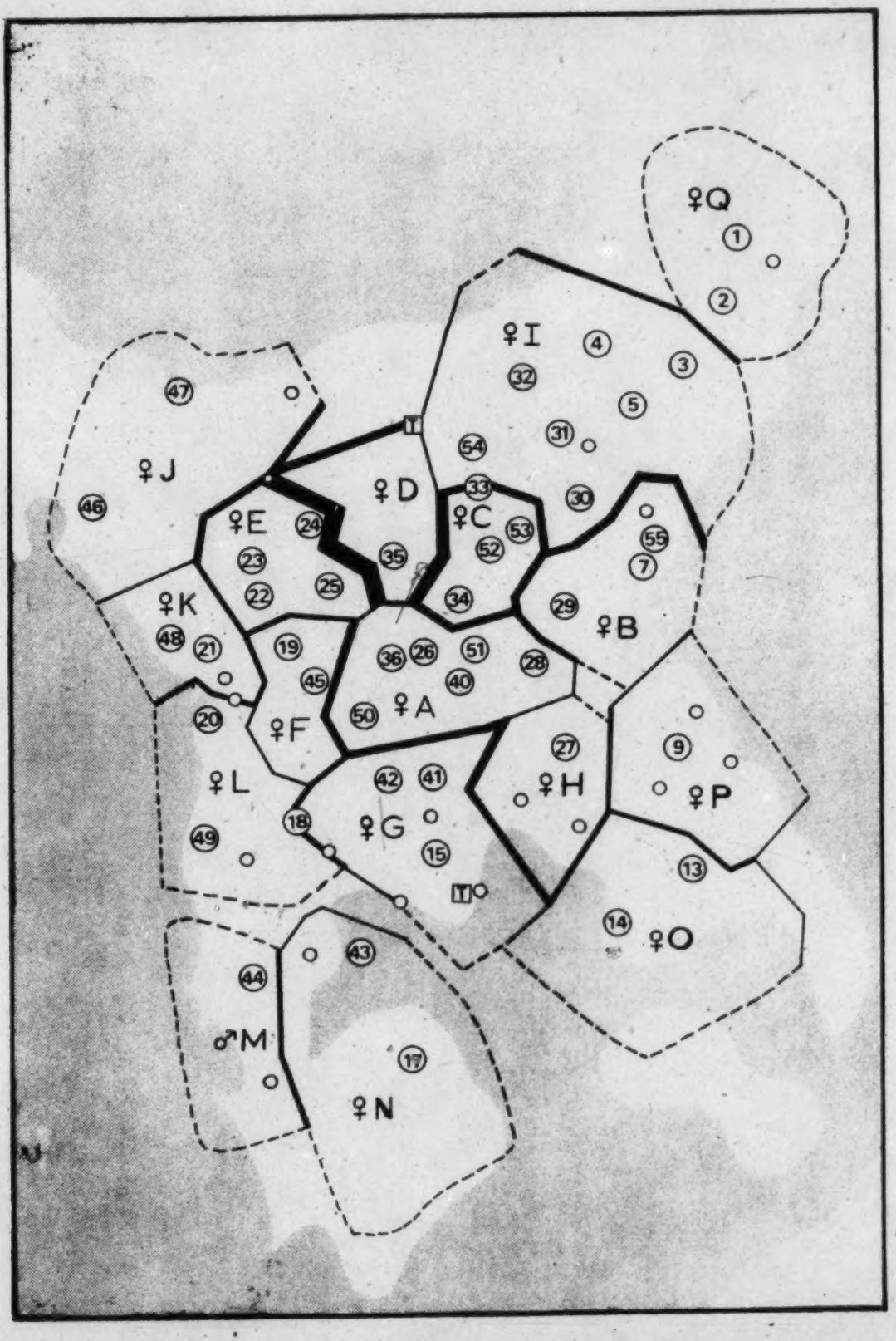
——— = 1 to 20

▬▬ = 21 to 40

▬▬ = 41 to 60

▬▬ = 61 to 80

▬▬ = 81 to 100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by fights. Attacks were the second most frequent type of interaction, followed by interactions involving only threatening or challenging. Fighting comprised slightly more than one-tenth of all interactions. The occurrence of active avoidance was least frequent, and in all cases it was the trespasser who left at the approach of the resident. This type of interaction usually involved a more peripheral animal trespassing in a more central area and leaving at the approach of the resident.

5. Interactions between age classes. There were no significant differences in the number of interactions between age classes but there were some differences in the components of the interactions between and within different age classes (Table 7). There were slightly more chases between animals of the same age class (adult-adult or yearling-yearling) than between age classes ($p<.10$). Between age classes, yearlings initiated more chases with adults than adults against yearlings ($p<.001$). Attacks were more frequent between adults and yearlings and among yearlings, and were infrequent between adults ($p<.001$). Again, yearlings more often initiated attacks against adults than vice versa ($p<.05$). Threatening and challenging was also slightly more frequent between age classes (adult-yearling) than within either age class ($p<.10$).

6. Interactions between neighbors and between non-neighbors. There were significantly more interactions between neighbors than between non-neighbors ($p<.001$). Chasing was more frequent between non-neighbors than among neighbors ($p<.001$) and the length of chases between non-neighbors was longer ($T=8.85$, $p<.001$). This cannot be explained on the basis of closer proximity of neighbors over non-neighbors since chases between neighbors and between non-neighbors often covered areas not

Table 7: Components of interactions between female ground squirrels within and between age classes. Interactions with the male were excluded from the calculations. There were seven adult and seven yearling females, giving an expected ratio of 3 : 7 : 3 for all components.

	Number of Interactions:			
Components	Between Adult ♀♀	Between Adult and Yearling ♀♀	Between Yearling ♀♀	
Avoidance	1	4	2	+
Threatening or Challenging	11	54	18	+
Chasing	71	116	58	+
Attacking	9	71	32	**
Fighting	22	52	29	n.s.

n.s. $p > .10$
\+ $p < .10$
* $p < .05$
** $p < .01$

defended by either animal. Also, a sizable portion of interactions between non-neighbors were initiated by an animal from within a neighbor's territory against a trespassing third animal. Chases involving the male were also longer than those among neighbors ($T=3.99$, $p<.001$). Attacking occurred more often between neighbors than between non-neighbors ($p<.001$), while the amount of fighting was nearly equal (Table 8). Very few interactions between non-neighbors were settled by threatening or challenging alone (6.5 percent) while these components alone comprised 19.6 percent of all interactions between neighbors ($p<.01$). There was no difference in avoidance between the two groups.

7. Nest sites. Transportation of live young to another nest site was observed for six of the 11 females that raised litters that appeared above ground (Figure 8). In one instance the entire litter was moved three times, although the number of young moved decreased with each shift in nest site. In two cases, the number of young moved corresponded to the total trapped at that site when the young emerged on their own. In three cases, only part of the litter was moved to a different nest site; two nests were frequented regularly by the female and young were trapped at both nest sites when they emerged. There was no noticeable tendency for nests to be located centrally or peripherally within a defended area and litter transport showed no consistent peripheral or central tendencies relative to the entire study area. Three litters were moved in a peripheral direction and three litters were moved to a more central position. The only consistent aspect of litter location was that nests appeared closer to minor burrow entrances than any other type. Bedding material was taken down a specific minor burrow entrance where young later emerged. Litters relocated were taken from one minor burrow entrance to another.

Table 8: Components of interactions between neighboring female ground squirrels compared to components of interactions between non-neighboring females during interval II, May 8 to May 30. Interactions involving the male were omitted from the analysis.

Component	Interactions between neighbors			Interactions between non-neighbors	
	Total number	% of total number		Total number	% of total number
Avoidance	10	2.3	n.s.	4	2.9
Threatening or Challenging	87	19.6	***	9	6.5
Chasing	180	40.5	***	94	67.6
Attacking	114	25.7	***	14	10.1
Fighting	53	11.9	n.s.	18	12.9
N =	444			139	

n.s. $p > .10$
\+ $p < .10$
* $p < .05$
** $p < .01$
*** $p < .001$

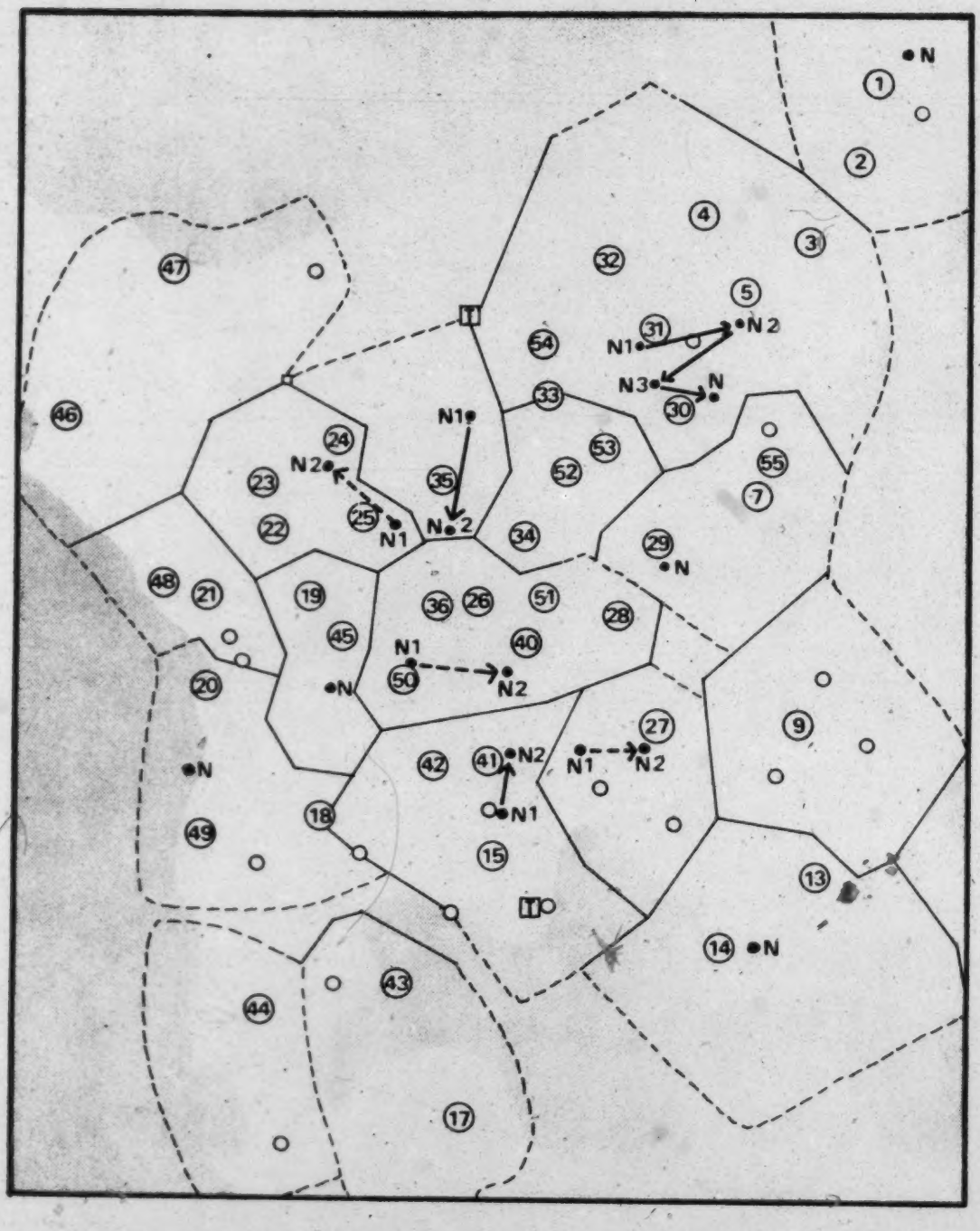

Figure 8: Litter transfer and location of ground squirrel nests during interval II, May 8 to May 30.

N = closest entrance to nest

⟶ indicates entire litter moved by female

- - - - ⟶ indicates part of litter moved and two nests maintained; live young trapped at both sites

Only after young animals had been above ground a few days did they appear at major burrow entrances.

8. Dominance index. Occasionally a resident was unsuccessful at excluding a trespasser and some individuals seemed to consistently initiate agonistic encounters outside their territory and elicited submissive postures from other residents. This appeared to be irrespective of differences between neighbors and non-neighbors and differences between age classes.

The classical concept of dominance implies the physical superiority of one animal over another and the possession of a territory is considered to enhance the dominance of a resident in encounters with a trespasser and influence the outcome of an interaction in favor of the resident. In instances where a resident shows deference towards a particular trespasser or is defeated in an encounter but not displaced from the territory, it may be that there is an additional aspect to the social organization of the population besides territoriality.

The possible existence of a hierarchy superimposed on a territorial colonial aggregation (called "territorial rank" by Davis, 1959) was investigated in the following ways. All decisive encounters in which a resident in close proximity to one of her major burrow systems was defeated by a trespasser were tabulated. The majority of these decisive interactions occurred in interval II and all the rest but three during the month of June (intervals III and IV). The results of these interactions are shown in Table 9.

All of these decisive interactions involved either chases or attacks and the resident either responded with a flattened submissive

Table 9: Decisive interactions between female ground squirrels.

Winner		Loser		
♀	Ring	♀	Ring	f[1]
A	1	E	2	1
A	1	F	2	1
A	1	G	2	3
A	1	B	2	1
A	1	H	2	2

N = 8

Winner		Loser		
♀	Ring	♀	Ring	f
A	1	K	3	2
A	1	P	3	1
A	1	L	3	1
A	1	N	3	1

N = 5

Winner		Loser		
♀	Ring	♀	Ring	f
D	2	J	3	3
B	2	K	3	1 *
E	2	J	3	1
B	2	P	3	2
F	2	L	3	1
G	2	I	3	1
H	2	P	3	1
B	2	I	3	2
H	2	O	3	1
F	2	K	3	1

N = 14

[1] f = frequency

*Except for this instance and the five recorded in the center column, all other decisive interactions occurred between females and their neighbors directly peripheral to or behind them.

posture or was chased from her own area. Relative to the total number of interactions, the percentage of decisive interactions was small (4.01 percent), but they comprised 10.07 percent of all attacks and 14.50 percent of all fights. In all cases listed, the "winner" was an animal from a more central ring, and the defeated resident an animal in a more peripheral ring. The most central female (A) defeated animals in rings two and three, and ring 2 females defeated animals in ring 3. There were only three exceptions to this pattern. Female B was defeated twice by female I at burrow #6, an active burrow in 1971 but not re-excavated in 1972. As a result of these two encounters, female B no longer approached animals that trespassed in the vicinity of #6 and trespassers were instead approached by female I. In the last case, female P was attacked by female O approximately six feet south of burrow #9 and flattened submissively after a fight. This interaction did not result in any noticeable shift in the areas defended by either animal.

9. Trespassing tolerance index. The second method used to determine the possible presence of a hierarchy was to consider instances in which a resident animal showed little or no hostile reaction towards a trespasser. In almost all cases, interactions occurred when one animal trespassed on the territory of another and usually resulted in the forced departure of the trespassing animal or defeat of the resident. However, there were 79 instances where neither of these results occurred and the trespasser was approached and occasionally threatened but no further interacting occurred. Occasionally the resident was threatened by the trespasser and would remain or move elsewhere within her territory. In none of these interactions did the trespasser retreat at the approach

of the resident and the animal would remain in the area without further conflict. None of these interactions seemed to effect a change in size of territory. The lack of hostile reaction shown by various animals resembles the inverse of that illustrated by decisive interactions. The most central female (A) remained without conflict with the resident in various areas in ring two 22 times and in ring 3, three times. In 29 instances, ring 3 animals did not dispute the trespassing of the neighbors ahead of them. Except for the lack of hostile behavior of ring 3 animals towards the most central female, agonistic behavior always occurred when the trespassing animal was a non-neighbor. In addition, ring 2 animals showed no hostile behavior toward the trespassing of neighbors to the side of them 13 times and ring 3 animals did not dispute the trespassing of neighbors at the side seven times. The only animal permitted to trespass without conflict in ring 1 was the yearling female C from ring 2. Tolerance by the central female for this particular yearling was recorded five times and in all five instances the yearling female flattened submissively at the approach of the central female. The two animals were not related and this type of relationship was not observed between any other animals on the study area.

10. Mobility index. The locations of nine of the 16 females were tabulated every ten minutes for the entire interval and the frequency of each animal in each of the three rings and within its own territory was calculated (Table 10). Frequency is expressed as a percentage representing the time (in minutes) in each location divided by the total amount of time each animal was present above ground during the hours of observation. The central animal spent the least time within her own defended

Table 10: Mobility index for nine female ground squirrels during interval II, May 8 to May 30. To meet the assumptions of analysis of variance, all figures were converted to arcsine of the percent for statistical t-tests.

		Percent of Total Time Spent in:		
	Female	own territory	neighboring territory	territory of non-neighbor
R. 1	A	67.72	16.71	15.56
Ring 2	* C	76.78	22.96	0.26
	D	72.04	16.04	11.95
	G	73.98	13.74	12.28
	H	72.01	21.07	6.92
Ring 3	* J	87.19	8.26	4.55
	* K	81.43	6.81	11.74
	O	78.24	6.28	15.48
	* P	88.38	8.26	3.36

* indicates non-lactating females

area. The amount of time spent within territories was higher for ring 2 animals and highest for animals in ring 3 ($t=3.60$, $p<.05$). This difference cannot be explained solely as site attachment due to the presence of young underground since non-lactating females in either ring spent proportionally more time in their own areas than lactating females in the same ring. There is also no significant correlation between the size of an animal's territory and the percent of time spent within or outside the territory. Ring 1 and 2 females spent more time in neighboring areas than ring 3 females, and the central female (A) spent the most time of any animal in areas occupied by non-neighbors. Ring 2 animals spent more time in neighboring areas than ring 3 females ($t=5.58$, $p<.05$) and in both rings, the animals spent less time in non-neighboring than in neighboring areas. Ring 2 females were involved in a higher number of interactions than females in ring 3 ($U=59$, $p<.01$) and the central female had an interaction rate 1.5 times that of the next highest female. This is to be expected, since as soon as an animal leaves its own territory, it is a trespasser on some other animal's, and the more time an animal spends outside its defended area, the greater the probability of involvement in an interaction.

Interval III, June 1 to June 14

Young ground squirrels were first observed above ground on May 26, and the last few days in May were occupied in trapping and marking juveniles. Throughout this interval, the juveniles wandered progressively further from their natal burrows during the day but returned to the nest site each afternoon and there was little decrease in their numbers during this interval.

1. Mobility index. During this interval, females showed an increase in time spent outside their defended areas, irrespective of ring position (Table 11). Of the females tested, all showed a decrease in the amount of time spent within their own territories relative to the previous interval ($t=3.03$, $p<.05$), but ring 3 females still spent slightly more time within their territories than did females in rings 1 and 2. From interval II to III, time spent in neighboring areas increased for three of four ring 2 females, but for only two of four ring 3 females. There was no significant difference in time spent in neighboring territories by ring 2 compared to ring 3 females for interval III. During interval III, five of the nine animals spent more time in non-neighboring than in neighboring territories. Compared to the previous interval, some of the animals were spending an increased percentage of time further from their own territories, since eight of the nine animals increased the amount of time spent in non-neighboring territories. All animals in rings 1 and 2 increased the amount of time spent in non-neighboring areas as did most (3/4) of the animals in ring 3 ($t=4.47$, $p<.01$).

Table 11: Mobility index for nine female ground squirrels: intervals II and III compared. To meet the assumptions of analysis of variance, all figures were converted to arcsine of the percent for statistical t-tests.

		Percent of Total Time Spent in:					
		own territory		neighboring territory		non-neighboring territory	
	Female	II[1]	III[2]	II	III	II	III
R. 1	A	67.72	59.26	16.71	12.59	15.56	28.15
Ring 2	C	76.78	55.97	22.96	35.82	0.26	8.21
	D	72.01	58.76	16.04	12.37	11.95	28.87
	G	73.98	71.43	13.74	15.87	12.28	12.70
	H	72.01	60.24	21.07	21.69	6.92	18.07
Ring 3	J	87.19	70.54	8.26	12.50	4.55	16.96
	K	81.43	59.37	6.81	4.68	11.74	35.93
	O	78.24	69.86	6.28	17.12	15.48	13.01
	P	88.38	83.80	8.26	2.82	3.36	13.38

[1] interval II, May 8 to May 30

[2] interval III, June 1 to June 14

2. Components of interactions. Residents still initiated the greatest proportion of interactions (78.45 percent) but the percentage of interactions initiated against trespassers from a third neighbor's area decreased to 8.83 percent (Table 4, pg. 33). The number of interactions initiated by trespassers increased from 9.55 percent in interval II to 12.72 percent in interval III (Table 3, pg. 31). In addition, there was a slight increase in the severity of interactions. Attacking was more frequent in this interval than in the previous one ($p<.01$) while the relative frequency of interactions involving only threatening or chasing declined ($p<.02$).

The length of chases between non-neighbors was still significantly longer than those between neighbors ($T=4.45$, $p<.001$). There were no differences in interaction components or frequency between or within age classes.

In 13 instances out of a total of 249 interactions, an interaction between adults occurred when a trespasser first attacked a juvenile within another animal's territory. A second female, usually the resident, became alert on hearing the cries of the juvenile and approached the first adult and attacked her or chased her out of the area. Cohesive nose-to-nose behavior followed between the resident female and her offspring. In two of the 13 cases, a female responded to the cries of a juvenile that wasn't hers; the adult female chased the trespasser, returned, and after a brief nose-to-nose encounter with the juvenile, chased it away also. In another two of the 13 cases, a juvenile strayed outside its mother's area and was attacked by the resident female. The mother of the juvenile in both cases trespassed and attacked the resident adult. No injuries to juveniles as a result of interactions with adults were

recorded.

3. Attempted resettlement. There are a number of factors involved in both the increase in mobility of the animals and the increase in the number of interactions initiated by trespassers. Once the young animals emerge above ground, they begin foraging for themselves and their nutritional demands on their mothers decrease gradually until they are completely weaned. Lactation places severe energy requirements on adult females and none gained weight from the time of parturition until the end of June. Lactating females spent a large portion of their time feeding and did not always forage within their own territories.

In addition, those females with only a few young surviving to emergence [F(AL2) and L(AL3)] and some of those which were never recorded as lactating [P(UX3), K(AX3), and J(YX3)] attempted to relocate elsewhere on the study area, and most of these new locations were more central than those which the animal previously occupied. Female J made frequent visits to burrow #26 but was constantly chased away. Female L spent a lot of time at #28 and P tried to remain at #29. Both animals retreated underground at the aforementioned burrows when attacked by the resident animals, and after a few days left the new sites at the approach of other animals. Female K moved to #32 and F moved to ten feet north of #27 and both remained in these new areas for over a week. They retreated underground at attacks from other animals and eventually successfully defended the new sites from trespassers. They were not successful, however, in defeating the residents that normally defended these burrow systems [I(AL3) and H(AL2) respectively] and were eventually chased out of these areas and returned to their previous burrow systems. The major burrow

system at #27 and was dug by female F in 1971, but at the end of the season she moved to the western edge of the study area and overwintered there; she made no attempt to re-settle at #27 until this interval.

4. Location of interactions. Both the increased mobility of the animals and the attempts of some females to resettle elsewhere resulted in a scattered distribution of interactions (Figure 9). Ring 2 females trespassing in ring 3, and ring 3 females trespassing in ring 2 resulted in the majority of interactions occurring in these areas, in contrast to the tight central distribution of interactions that occurred in interval I. The concentration of interactions around specific burrow entrances (#26, 27, 28, 29, and 32) reflected the conflict resulting when five of the adult females attempted to resettle at these sites.

The adult male disappeared from the population during this interval and was not recorded after June 5. This was earlier than expected since the few males present in 1971 were present until the last week in June.

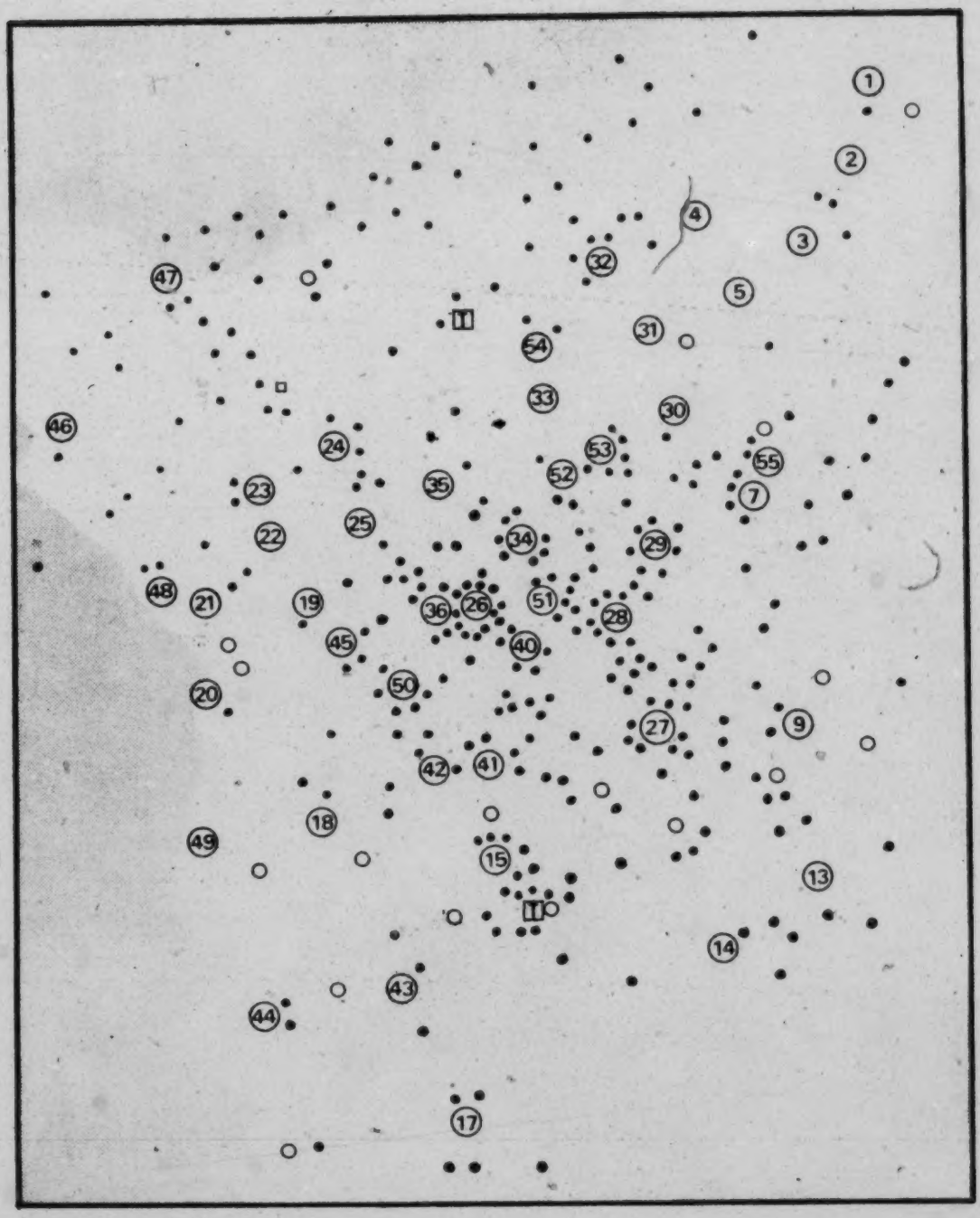

Figure 9: Location of interactions during interval III, June 1 to June 14. Each solid dot represents one interaction between two ground squirrels.

Interval IV, June 15 to June 30

On the afternoon of June 14, a weasel invaded the eastern end of the study area and killed two adult ground squirrels [I(AL3) and B(YL2)]. This left two adjacent areas without residents and the responses of the remaining ground squirrels to the newly vacant areas altered the previous social situation. The interval divisions were based on major changes in the seasonal biology of the ground squirrels so this latter interval designation is, in a sense, arbitrary. Had predation not occurred, the social organization in this interval would have been included in interval III.

1. Interactions between non-neighbors. Compared to interval III, there was a decrease in the relative number of interactions between neighbors and an increase in the relative number of interactions between non-neighbors ($p<.001$). The increase in the relative number of interactions between non-neighbors was probably due to two main factors. The animals appeared to spend even more time outside and further from their territories, and animals from all over the study area were observed in the areas left vacant by the loss of the two females. Since most of the animals had to move through the territories of non-neighbors to reach the vacant areas the probability of interactions with non-neighbors along the way was increased. The weasel paid frequent visits to the study area following the successful capture of the two females, and on June 19 moved three kits to burrow #24 and lived on the area until June 28. After June 28, the weasel moved her kits elsewhere but continued to visit the study area at weekly intervals. The ground squirrels continued to chase non-neighbors over longer distances than neighbors ($T=3.38$, $p<.001$) but would

chase the weasel over even greater distances, sometimes traversing the entire study area. To evade harassment by adult ground squirrels, the weasel would frequently dive down a ground squirrel burrow, reappear at another entrance and move off without inciting pursuit. Chases with the weasel were accompanied by the alarm calls of most nearby squirrels. The alarm calls served to alert the resident of an area who usually arrived at the conclusion of a chase after the weasel had gone underground and when only the squirrel that had chased the weasel was present. Since the chases with the weasel covered longer distances than chases among squirrels, the trespassing squirrel was usually not a neighbor of the resident and an interaction between non-neighbors frequently followed a chase with the weasel. It is interesting to note that although the weasel was almost always chased when she appeared above ground, no adult ground squirrel would continue the chase underground, even if the chase concluded at a burrow system she usually defended. Considering their relative lengths and weights, the weasel may have an advantage of greater maneuverability underground. In August, 1971, a juvenile male pursued a weasel underground and was never seen again.

2. Resettlement. More interactions were initiated by an animal while in a neighboring area during this interval than during interval III ($p < .001$) and these interactions were initiated primarily against trespassing non-neighbors rather than against other neighbors ($p < .01$) (Table 4, pg. 33). This was in part due to the increased mobility of all the animals and to the influence of the weasel on distance of chases. An important additional influence was the attempts of two animals to resettle in the area left vacant by females I and B. Female K(AX3) who had

previously attempted to move to #32 continued to visit that portion of the study area and after the deaths of the two females moved to a minor burrow entrance between #29 and #53. She did not remain there more than a few days and eventually returned to her previous site. Female Q(UL3), who had previously never been observed closer to the center than burrow #7, moved from her previous position near burrow #1 to occupy and successfully defend burrow #29. Although female C(YX2) expanded her territory to include burrow #54, no squirrels moved outward to occupy the rest of the space left vacant by female I. The only animal to markedly change her location was female Q who moved from a peripheral to a more central position in spite of the fact that her litter remained near burrow #1. This centripetal movement after the removal of a resident further supports the observed tendency of *S. richardsonii* to congregate in a central location, and implies, perhaps, a preference for central over more peripheral positions.

3. Components of interactions. There was no difference in the severity of interactions between neighbors and non-neighbors, but the severity of interactions diminished between interval III and IV (Table 3, pg. 31). In interval IV, fewer interactions involved fighting ($p < .001$) and significantly more interactions involved only threatening or challenging ($p < .001$) than previously. Proportionally more interactions were characterized by avoidance ($p < .01$) where a trespasser left an area at the approach of a resident and no pursuit ensued.

Interval V, July 1 to July 30

1. Torpidity. During interval V, the number of animals active above ground declined steadily as the remaining adult and yearling females disappeared for their annual episodes of torpidity. All females which did not raise a litter disappeared earlier than females that raised litters and there was no overlap between the two groups. There was a high degree of correlation ($r=-.89$, $p<.001$) between the relative weights of the animals as early as June 21 and the order in which animals disappeared for torpidity (Table 12).

The overwinter location of most females was somewhere within their own territories and in some cases the precise location was noted as a result of the sequence of events preceding the onset of torpidity. Individuals were observed carrying bedding material to specific locations; in all cases the entrance used for access to the presumed chamber was a minor burrow entrance. Within a week of final disappearance, the individual animals emerged later in the morning than others and retired earlier, always emerging from and retiring down the same minor burrow entrance. After the final appearance above ground, the burrow entrance was plugged with dirt. However, this last step was not irreversible. Two animals, females K and H both dug through the dirt plugs at their respective burrow entrances and spent an additional morning feeding. Upon retiring, the dirt plugs were replaced and the animals were not seen again for the rest of the season. Female K was an exception to the general tendency of individuals to overwinter within their own territories. She had attempted unsuccessfully to resettle between burrows #29 and #53 during interval IV and returned to this area during her last week above ground. Despite antagonistic

Table 12: Relationship between weight, reproductive condition, and order of entrance into torpor (r = .95). Data were incomplete for females D and Q.

Female	Weight on June 21	Last seen above ground on	Reproductive condition [1]
P	472	6 / 27	X
J	470	6 / 30	X
K	447	6 / 30	X
N	454	7 / 4	X
C	398	7 / 5	X
G	431	7 / 14	L
O	396	7 / 14	L
L	385	7 / 18	L
E	391	7 / 19	L
A	366	7 / 21	L
H	370	7 / 28	L

[1] X = non-lactating (i.e. did not raise a litter)
L = lactating

encounters with female Q, K remained in the area and overwintered there.

2. Components of interactions. There was a significant decrease in the frequency of interactions in this interval compared to the previous one ($p<.001$). The decrease in the number of interactions is directly related to the decline in the number of animals still above ground ($r=.80$, $p<.01$). There were no interactions after July 17 although five animals were still present. There was no difference in the severity of the interactions compared to those of the previous interval. Interactions characterized by threatening or chasing occurred more often than those involving attacking and fighting.

3. Greeting and allo-grooming. A number of instances of greeting and allo-grooming were observed between pairs of adults and yearlings. This type of interaction is common between adult females and their young of a given year (Steiner, 1973; Sheppard and Yoshida, 1971) and there is some evidence for recognition following hibernation between a female and her young of the previous year (G. Michener, 1972). During this interval, two greeting sequences involved two different pairs of adult females (L and A; L and H), three sequences involved an adult female (L) and an unrelated female yearling (G), and two greeting sequences involved an adult female (H) and her yearling daughter (O). On two occasions greeting was observed between two non-related yearling neighbors (E and J). Greeting was accomplished by mouth to mouth contact and one or both animals usually held the mouth slightly open. It appeared investigatory in nature, but not as prolonged or extensive as that described for *Cynomys ludovicianus* (King, 1955) or for adult and young *S. richardsonii* (G. Michener, 1972). Each pair for which this behavior occurred involved a

central animal (from ring 1 or 2) and a more peripheral animal, and in every case the interaction was initiated by the peripheral animal against a trespassing central animal. In three instances, greeting was followed by allo-grooming. Female O greeted her mother trespassing at #14 and groomed the region near her head and neck for nearly five minutes. On two different occasions, female L groomed the more centrally located yearling G near #18. These grooming bouts lasted longer than five minutes and L appeared to groom the head region, neck and back of G with her teeth. Since greeting and grooming have been observed between both related and non-related individuals it seems to represent a behavior not functioning purely in sibling or mother-young recognition. A broader interpretation, an implication of dominance relationships or friendly behavior is consistent with the trespassing tolerance index mentioned in interval II, where peripheral animals tolerated trespassing by more centrally located individuals. In the interactions involving greeting and grooming, it was the resident peripheral animal in all cases which initiated the grooming against a trespassing, more centrally located female. There were no differences related to the age classes of the animals involved, nor was this type of interaction limited only to related individuals.

SUMMARY OF SOCIAL ORGANIZATION

1. Female Richardson's ground squirrels occupy nearly exclusive spatial territories within a colony although trespassing by individuals occurs. Although the male ranged over the whole study area, he only defended a small area on the periphery. Territorial boundaries were most distinct during interval II when young animals were born and living underground. Female territories are more than just nidic territories since they include a number of major burrow systems and encompass an area greater than a specific nest site; they are however, "burrow-centered".

2. The territories in this colony were arranged spatially in a series of concentric rings with the territory of a single female in the center, the territories of seven females comprising the next ring, and those of eight females and the one male comprising the most peripheral ring.

3. The tendency of female ground squirrels to seek a central position in the colony was supported by the following:

A. The majority of interactions during the period of settling in were concentrated towards the center of the study area.

B. Two animals which hibernated on the periphery successfully settled in ring 2. No animals moved from a more central to a more peripheral area.

C. During interval III, five females attempted to resettle in a more central location (but were unsuccessful).

D. Following the deaths of two females in mid-June, one area left vacant was occupied by a more peripheral female. No central

animals moved outward to occupy the remaining vacant area.

E. There was a significantly higher density of animals centrally than peripherally.

4. During interval I, there were significantly more interactions between yearlings than between adults and yearlings or among adults. For the rest of the season, there was no difference in the frequency of interactions within or between any age class. During interval II, there were more chases between animals of the same age class (A-A or Y-Y) than between age classes. Attacks were more frequent between adults and yearlings and among yearlings than among adults. During interval I, there were more interactions between the male and females of both age classes than expected by chance.

5. There were more interactions between neighbors than between non-neighbors. While the male was present, there were more interactions with the male than with non-neighbors. Non-neighbors and the male were chased over longer distances than neighbors. Chasing was the most frequent type of interaction between non-neighbors but both attacking and interactions settled by threatening only were more frequent between neighbors.

6. Residents initiated the greatest percentage of interactions during all intervals. Percentage of interactions initiated by trespassers was highest during the period of settling in (interval I) and during the periods of attempted resettlement (intervals III and IV). The percentage of interactions initiated by a resident while within a neighbor's territory was highest during interval IV, the period of attempted

and successful resettlement.

7. Chasing was the most frequent component of all interactions until interval V, when interactions involving only threatening or challenging were most frequent. Attacking and fighting occurred most frequently during the period of attempted resettlement (interval III) and then declined for the remainder of the season. As the frequency of attacking and fighting declined, the percentage of interactions characterized by avoidance or by threatening or challenging rose correspondingly.

8. Evidence for the presence of a hierarchy superimposed on a territorial colonial system is provided by results of the dominance index and the trespassing tolerance index. The most central female defeated resident animals in rings 2 and 3, while females in ring 2 were able to defeat more peripheral resident neighbors. Trespassing by the centralmost female occurred without hostile reaction from resident animals in rings 2 and 3, while ring 2 animals trespassed without conflict only in some adjacent areas in ring 2 and, to a greater extent, in territories of peripheral neighbors in ring 3.

9. All females spent the greatest percentage of time within their own territories during interval II. Thereafter, all animals spent progressively more time outside their own territories. Central females spent more time outside their own territories than peripheral females. There is some indication that animals spend more time further from their territories after interval II.

RESULTS

PART II: ACTIVITY

Introduction

Eleven different types of activity were tabulated and compared for central and peripheral animals. The number of subdivisions of activity were limited to those gross activities observable in a field situation with the aid of binoculars. Since it was imperative to record the behavior of all the animals on the area simultaneously, detailed components of each activity were not included (with the exception of the components of social interactions). Seasonal variation was tabulated by intervals, since it was expected that changes in the biological condition of the animals would be reflected in changes in various types of activity. Although the observation times were constant for each day, not all the animals were visible all the time. For purposes of comparison, all absolute durations of activity (in minutes) were converted to percent of total time above ground for each animal for each interval. Actual time spent above ground and percentages of this time devoted to each activity are given for each animal in appendix II. In statistical analyses, data for the central female in ring 1 were combined with those for females in ring 2, and these totals were compared to data for ring 3 females.* The Mann-Whitney U-test was used throughout this section (unless otherwise indicated) to compare aspects of activity between the two groups. Additional activity comparisons were made between yearling and adult females, irrespective of ring position. Data on the single male ground squirrel were omitted from the statistical analysis of activity.

* see remark page 121

The types of activities tabulated for comparison may be grossly subdivided into two categories: non-social activity, such as feeding and self-grooming which are necessary for the preservation of the animal as an individual, and social activity such as marking and interacting which involve other members of the group to a greater or lesser degree. A brief description of each of the activities involved is followed by the statistical comparisons of these activities among different subgroups of the ground squirrel colony.

Non-social Activities

1. Feeding. Ground squirrels bit off and ingested short grasses and small leafy plants without using the forepaws. The animals were not stationary during feeding but moved short distances after every few mouthfuls. Occasionally the forepaws would be used to bend down the head of a taller stalk of grass. In the two instances a ground squirrel was observed to capture and eat other animals, the forepaws were used to catch the animal (a butterfly) or pin it to the ground (very small frog). The duration of feeding activity recorded included ingestion as well as the limited amount of locomotion between mouthfuls.

2. Food gathering. Infrequently an animal would bite off pieces of grass or small leafy plants and accummulate them in its mouth and cheeks without chewing or swallowing. When a sufficient amount was collected, the animal would go underground and not reappear for some time. This type of feeding occurred most frequently just prior to the cessation of above ground activity during the hottest part of the day or just before a heavy rainfall. Food gathering may follow a period of regular feeding

or any other activity, or the animal may make a special trip above ground to gather food. Presumably the food is eaten while the animal is underground.

3. Digging. Old burrows are widened and new burrows begun initially by pawing at the ground with the forefeet. By this action, most of the dirt is thrown beneath the body. After a small pile accummulates, the animal uses its hind feet to push the dirt further from the burrow entrance. After several hours of such activity, a mound of dirt up to two meters in diameter surrounds the entrance. If the mound is very steep, ground squirrels will move dirt away from the entrance by pushing with the forehead and top of the skull which results in a leveling of the top of the mound. Digging movements were also used infrequently to obtain plant parts at ground level (or roots?) for food or for bedding material. Digging in this context was of extremely short duration (less than one minute) and was considered part of feeding or bedding material collecting rather than digging activity.

4, Bedding material collection. Using the forepaws, an animal would dig briefly at the base of a clump of dry grass and remove pieces by tearing them off with the teeth in a rapid, jerky motion. The long pieces would be manipulated with the forepaws and packed sideways behind the incisors. After repeating this process two or three times, the animal would deposit the material down a burrow and reappear almost immediately for another trip. Both the time spent gathering the material and the traveling to and from the burrow to deposit the material were tabulated as bedding material collection. Although this activity superficially resembles food gathering, several unique aspects of bedding material

collection made it easy to distinguish the two activities in the field. Animals with bedding material frequently paused under the observation towers on their way to their burrows. From this close range, it was apparent that bedding material was always dry grass with only the occasional green blade in the bunch. A ground squirrel trapped while gathering food disgorged the contents of its cheek pouches and all the plant pieces were fresh and green, except for a few seeds. Bedding material was collected over a period of several trips while trips for food gathering seldom occurred more than once at any one time. Lastly, differentiation of the two types of activity was simplified since gathered food never protruded from the animal's mouth, whereas bedding material was always visible when it was being transported. These differences are in agreement with observations made by G. Michener in Saskatchewan (pers. comm.).

5. Grooming. Areas that could be reached with the mouth, including the limbs, belly, anal region and tail, were cleaned with the tongue. Frequently the animal would use its teeth to nibble at a spot in its fur. Ground squirrels used their forepaws in a washing motion over their necks, heads, and ears, areas that could not be reached directly with the tongue. Both fore and hind feet were used to scratch dorsally, ventrally, and behind the ears. Although grooming is essentially a non-social activity, it occurred in several social contexts as well. A very brief bout of grooming frequently occurred following agonistic contact with another animal. Since the duration of activity in this context was at most a few seconds, it may be more appropriately considered a displacement activity. As such, it was not tabulated under grooming activity. Allo-grooming among adults and yearlings also occurred in the

interval prior to hibernation. Although allo-grooming may, in fact, have maintenance functions, the occurrence also had strong social implications. These infrequent periods of allo-grooming were excluded from the tabulation of grooming time.

6. Sunning. On cool, sunny days or days following a rain, ground squirrels would sit or lie on the burrow mounds in one of two postures. If the ground was damp, the ground squirrel would sit hunched over with all four feet close together and with its back to the wind. If the air was cool but the mound was dry, the squirrel would lie with its belly against the substrate, its hind legs extended backwards, and ventral surfaces of the feet facing upwards. The latter posture could facilitate warming the animal since the dark substrate would hold heat. The hunched posture may aid in conserving heat or present least contact with moist substrata. In both sunning postures the animals appear quite relaxed and frequently their eyes were partially or completely closed.

Social Activities

1. Alert behavior. A degree of watchfulness is common to all ground squirrel activities, but alert behavior is distinguished by lack of locomotion and a rigid body posture. There are a variety of alert postures including prone, upright crouched with the weight supported by the legs and posterior, and upright extended with the body weight supported by the hind legs alone. In all variations of alert posture the head is held higher than the rest of the body. These postures were used during alarm calls, at the approach of another ground squirrel, or at the approach of a potential predator.

2. Investigating. Ground squirrels displayed considerable interest in burrow entrances or other specific locations visited or marked by other individuals. Support for the association of investigating with the relatively recent presence of other ground squirrels is provided by the close temporal relationship between the activities of one ground squirrel followed by investigative behavior in the same area by a second ground squirrel. The information derived may be both olfactory, when investigating follows marking by a first animal, and auditory, if the first animal is in a burrow but out of sight. Investigation of a novel object was not included in this category. Investigatory behavior was common both within and outside of an individual's own territory and may be broadly interpreted as the reception of information concerning the recent presence or absence of another animal at that location.

3. Visiting burrows. An animal would disappear down a burrow entrance and reappear at the same entrance within a few seconds. Investigatory behavior sometimes preceded visiting, but the two activities were not consistently sequential. Visiting occurred at burrow sites both within and outside an individual's territory.

4. Marking. Marking is characterized by the deliberate wiping of the oral angle, the cheek region between the angle of the jaws and the base of the ear, and sometimes the lateral surface of the body on a projecting portion of the substrate. Surfaces frequently marked included burrow hills and entrances, wooden stakes used to indicate burrow locations and grid positions (for mapping of the area), and large rocks. Marking among *S. richardsonii* appears very similar to that described by Steiner (1973) for *S. columbianus* and *S. undulatus*. In *S. richardsonii*,

the angle of the mouth is known to contain secretory apocrine glands (Quay, 1965). The function of these glands is still under investigation, but it is thought that such scent marking functions in olfactory group and quite possibly individual, communication or recognition (Ralls, 1971).

5. Interacting. When the behavior of one or more ground squirrels has a direct and immediate effect on the behavior of another animal, this constitutes an interaction. The components of an interaction range from avoidance to the most potentially injurious type of agonistic contact, fighting. These components were considered individually in determining the social organization within the colony. For purposes of quantitative comparison between animals of different social status, the percentage of total time spent in all types of interactions was combined for analysis.

Activity Results

1. Feeding. The predominant activity of ground squirrels throughout the season was feeding. After prolonged periods of inactivity due to unfavorable weather, feeding was always the first activity of any duration to occur upon emergence. From field observations, it appeared to be the most consistent activity upon emergence in the morning, regardless of the season, and usually extensive feeding preceded retirement to burrows in the evening. There were no significant differences between central and peripheral females in the percentage of time spent feeding for any interval (Figure 10).

The male increased the amount of time spent feeding during each of the intervals he was present in the colony. The total amount of time he spent feeding was lower than the averages for both groups of females in both intervals I and II, but was considerably higher than the percentages for both groups of females in interval III, when feeding by females comprised the lowest percentage of total activity of all intervals. Due to the small sample size of males (one), the results were not compared statistically, but the large quantitative difference is undoubtedly due to the difference in onset of torpor between adult males and females. The male disappeared after June 5, but females did not begin torpor until June 27. The percentage of time spent feeding follows a similar trend for both the male and females, except that the females have a longer season of above ground activity so increase in feeding prior to disappearance underground is delayed.

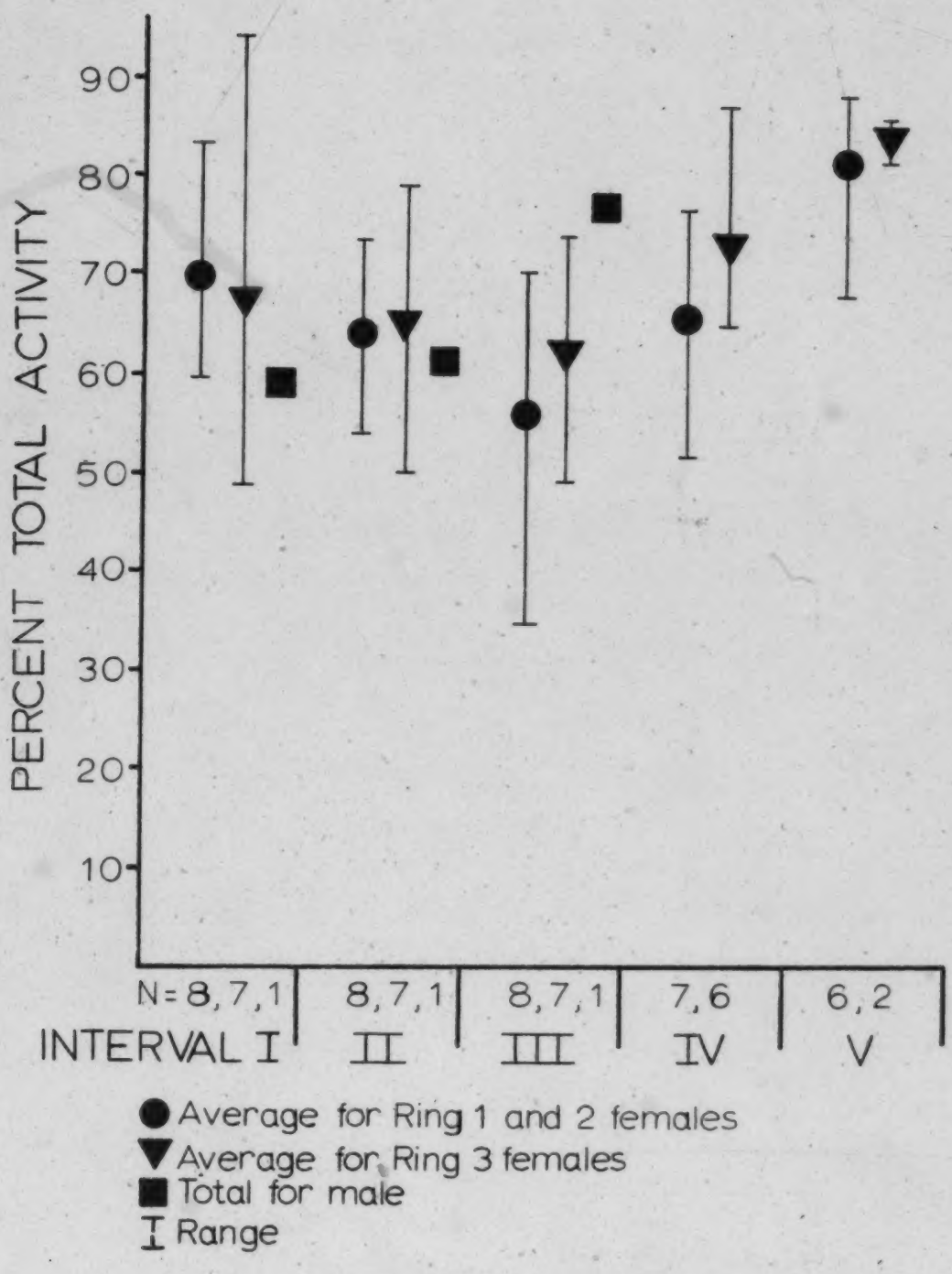

Figure 10: Feeding activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. N indicates sample size for each group.

2. Food gathering. Food gathering usually occurred just prior to the hottest parts of the day. This activity presumably allowed the animal to continue feeding while at the same time avoiding the danger of heat stress. Because of the association between high temperatures and food gathering activity, the complete lack of any such activity during interval I is understandable, since the maximum daily temperatures seldom reached 55°F. While ring 1 and 2 females had a greater occurrence of food gathering during intervals II, III, and V and ring 3 females had a higher percentage of food gathering in interval IV, the differences between the two groups of females were not significant (Figure 11). The male was only observed to gather food during interval II. For all animals, the time spent food gathering was greatest in the interval preceding the interval in which they began torpor. This would indicate that food gathering may be an asset in gaining weight prior to dormancy although there is the possibility that some of this food may remain underground and serve as a cache for the brief periods of arousal during hibernation.

3. Digging. The occurrence of digging for all animals declined from the highest percentages in interval I to the lowest in interval IV; digging was not performed at all during interval V (Figure 12). Only in interval I did digging percentages for peripheral females exceed that for central females. This was probably due to the fact that fewer burrow systems existed on the periphery of the colony from the previous year, so that animals living on the periphery had to dig more major and secondary burrow systems for shelter than animals in the center, where digging activity was more confined to re-excavating already existing burrow systems. Major and secondary burrow systems were created in all rings,

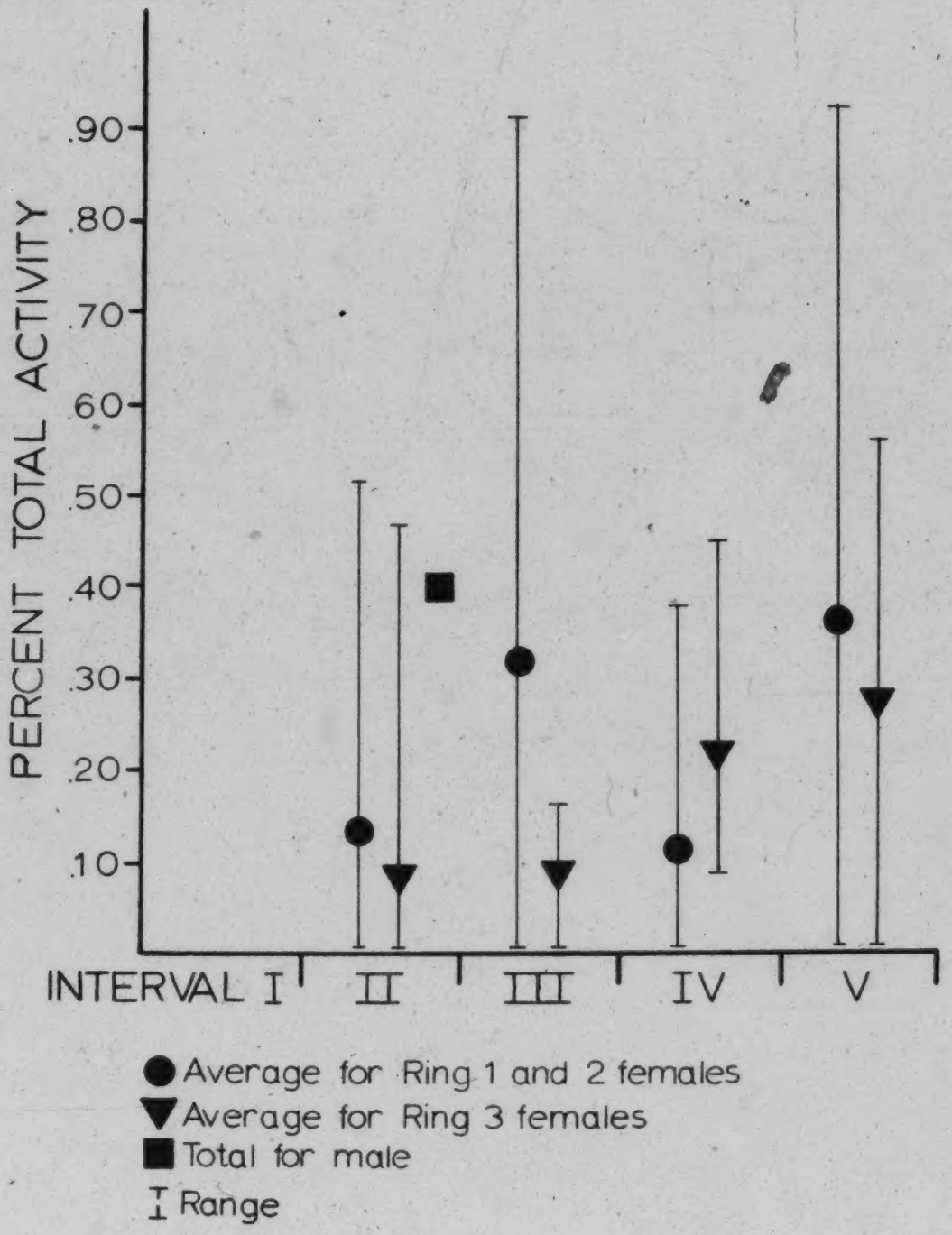

Figure 11: Food gathering activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

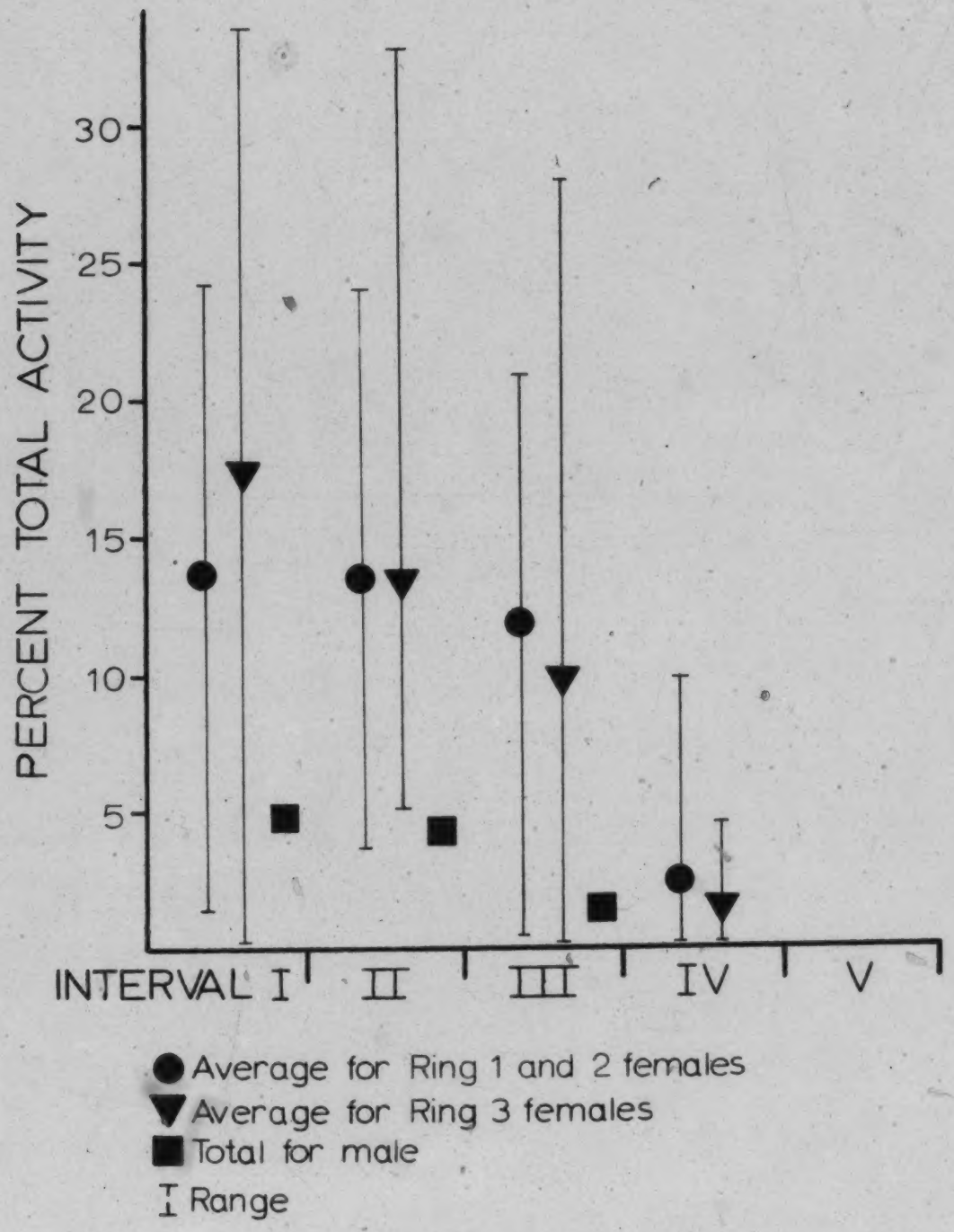

Figure 12: Digging activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

but over twice as many were created in ring 3 than in rings 1 and 2 (Figure 13). However, there was no statistically significant differences in digging activity between central and peripheral females during any interval throughout the season. The male did less than half as much digging as either female group in any interval. This is as expected, since he defended fewer burrow systems than any female and did not require additional space underground for a litter.

4. Bedding material collection. There was an appreciable difference in bedding material collection between central females and peripheral females (Figure 14). Among central females, the percentage of total activity time devoted to collection of bedding material increased progressively during the first three intervals of the season and was consistently higher than that for peripheral females. The differences for interval II were slightly significant ($p < .10$) and approached significance for interval III ($p < .20$). Bedding material collection for peripheral females decreased progressively throughout the season. The least amount of bedding material collection among both groups occurred during intervals IV and V, and the slight differences between the two groups was not significant.

5. Grooming. Generally, the percentage of time spent grooming increased with each interval with two exceptions (Figure 15). The male showed the highest incidence of grooming during interval II, the interval prior to his disappearance. Grooming increased among peripheral females for the first four intervals and then decreased during interval V. Grooming among central females increased progressively throughout the season,

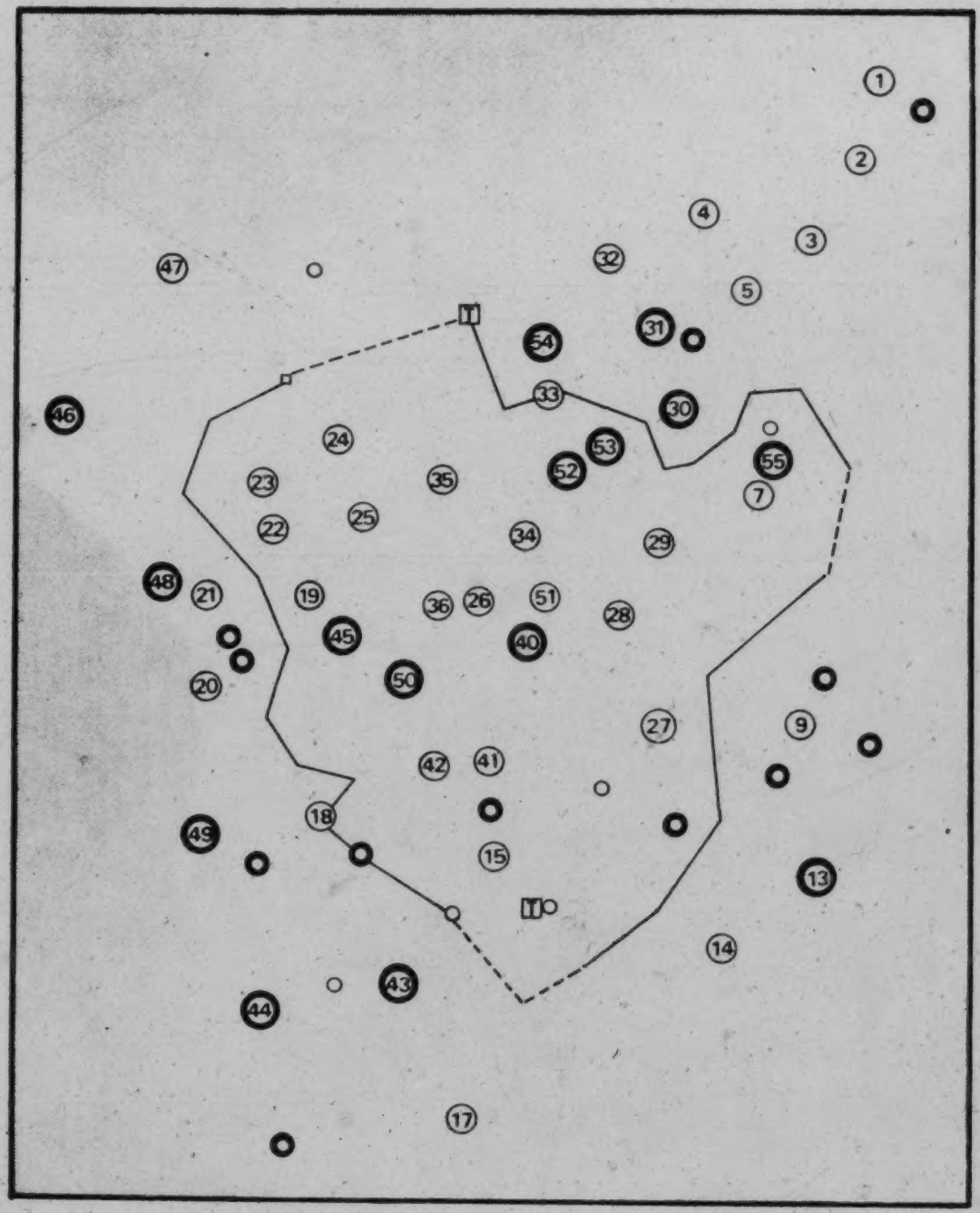

Figure 13: Burrows enlarged or created in 1972. Burrow entrances surrounded by heavy black lines were first excavated or enlarged from minor burrow entrances to their present size during 1972. Lines enclose the territories of central animals.

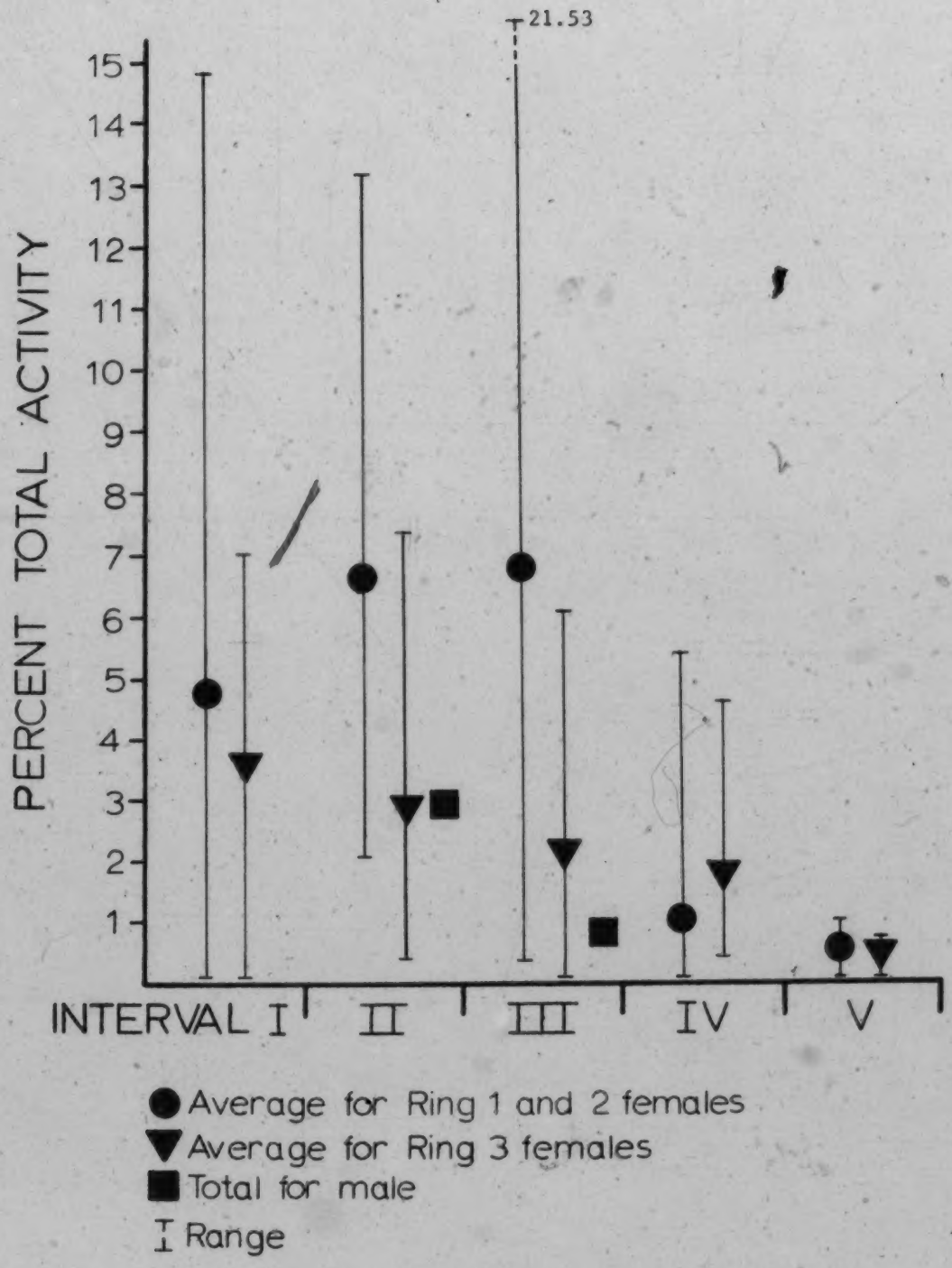

Figure 14: Bedding material collection: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

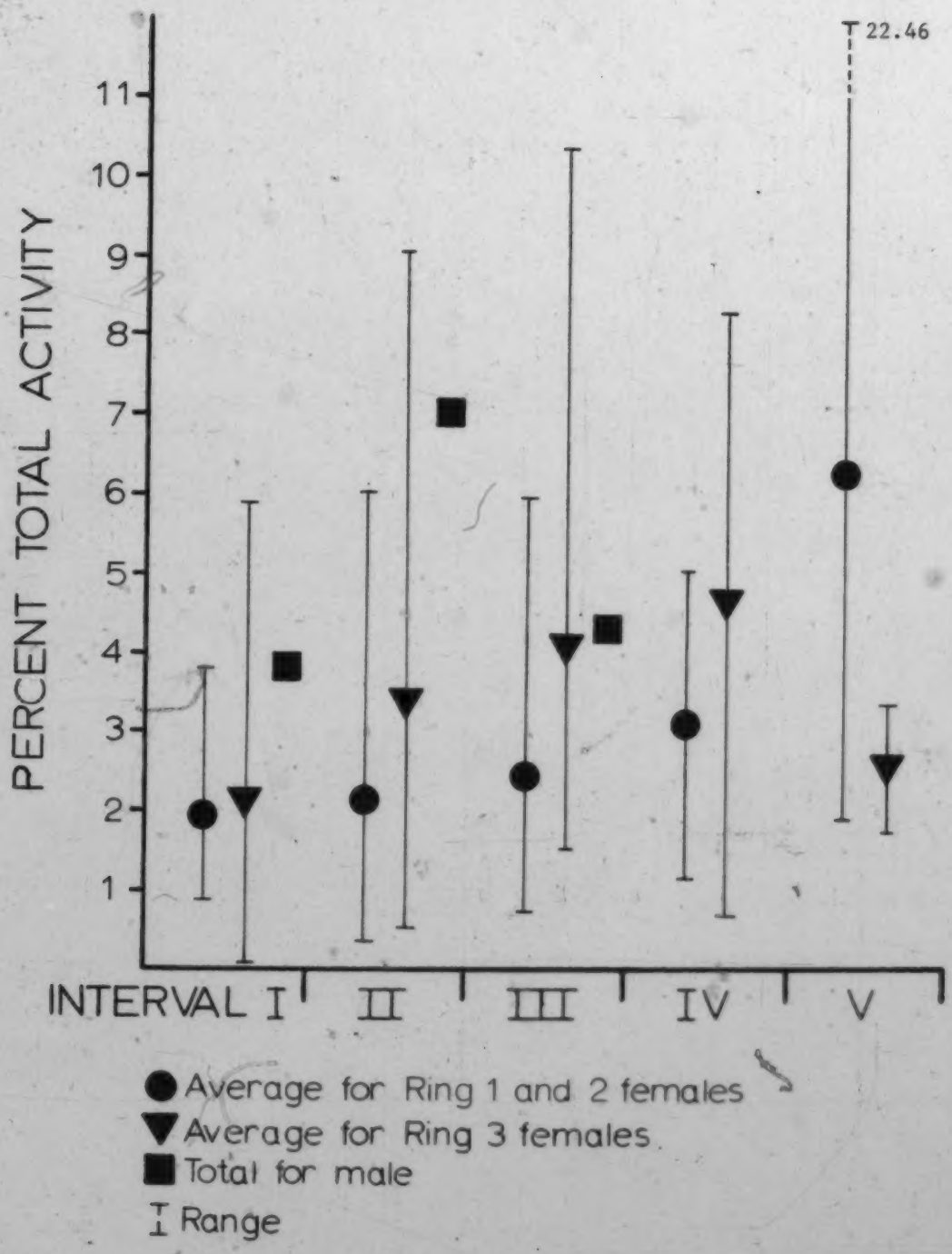

Figure 15: Grooming activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

with the highest percentage during interval V. The trend was the same for the male and both groups of females. That is, since peripheral females tended to enter torpor at the end of interval IV and early in interval V, and since most central females did not begin torpor until the middle of interval V, it would appear that the percentage of time devoted to grooming is highest for each group just prior to torpor. Throughout the first four intervals, peripheral females spent a consistently higher percentage of total activity time on grooming than central females. Only during interval V did central females have a higher incidence of grooming than peripheral females. However, none of the differences between the two groups were statistically significant.

6. Sunning. Among females, less than one percent of total activity was devoted to sunning during any one interval (Figure 16). Differences between central and peripheral females were not significant. While never a major activity, sunning was six times greater for the male during intervals I and II than for either female group.

7. Alert behavior. The percentage of total activity time comprising alert behavior increased during each interval for both groups of females throughout the season except for interval V, when it declined (Figure 17). Peripheral females showed a slightly greater percentage of prolonged alert behavior than did central females except during interval IV. The increase in alert behavior for central females during this interval was most probably due to the residence of the weasel and her kits in the central area of the colony. It is assumed that the object of alert behavior is the detection of predators and/or other ground squirrels. In spite of the consistent differences in alert behavior between

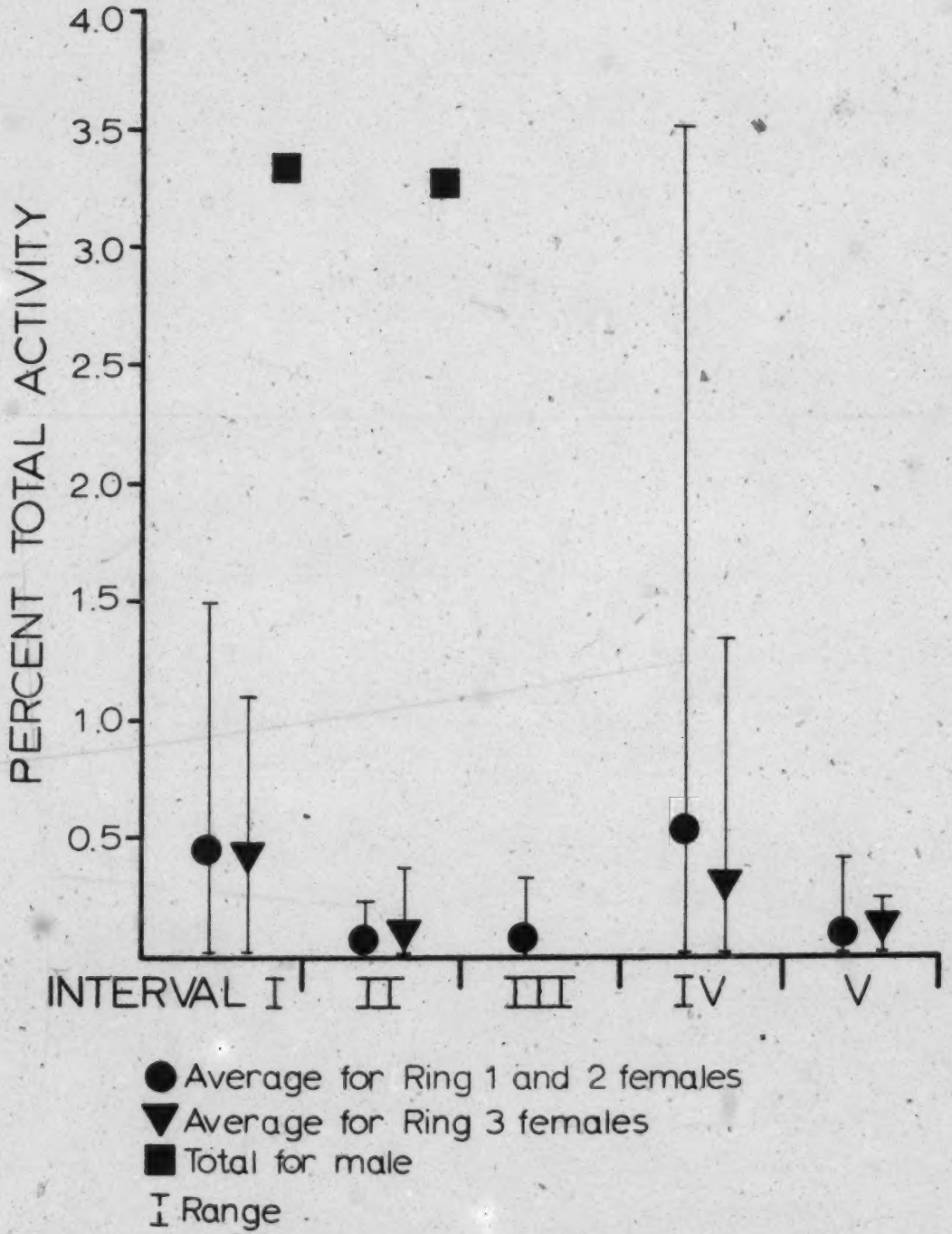

Figure 16: Sunning activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

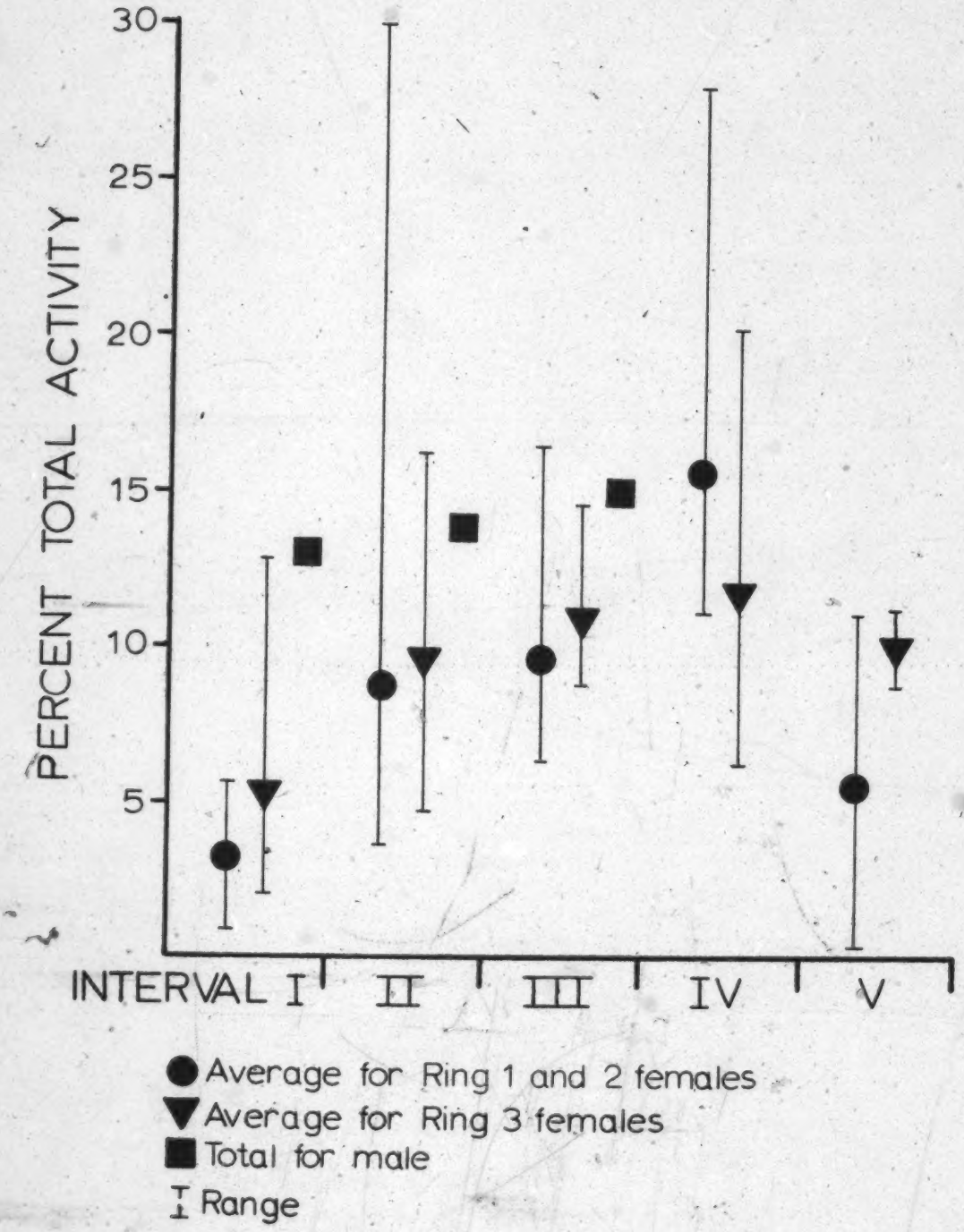

Figure 17: Alert activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

central and peripheral females, the results were not statistically significant for any interval.

The male showed the greatest amount of alert behavior of any animal during the three intervals he was present in the colony. A high degree of alert behavior is consistent with his peripheral location within the area of the colony, but the amount of alert behavior was considerably higher than that of peripheral females.

8. Investigating. The percentage incidence of investigative activity increased seasonally through interval IV and declined to a very low level during interval V (Figure 18). Investigating time that preceded marking or visiting was categorized under either of the other two activities since the actual duration of the activity was so brief. Only investigating activity not followed by marking or visiting is considered in this category. There was no consistent trend for either central or peripheral females throughout the season and differences which occurred between the two groups within each interval were not significant. Investigating by the male was highest during interval I, not observed during interval II, and considerably less than either female group during interval III.

9. Visiting burrows. Among females, the amount of time spent visiting was highest during intervals III and IV (Figure 19). The greatest amount of visiting by peripheral females occurred during interval III when several were attempting to resettle in more central positions. Among central females, the percentage of visiting increased progressively until interval V, when it declined.

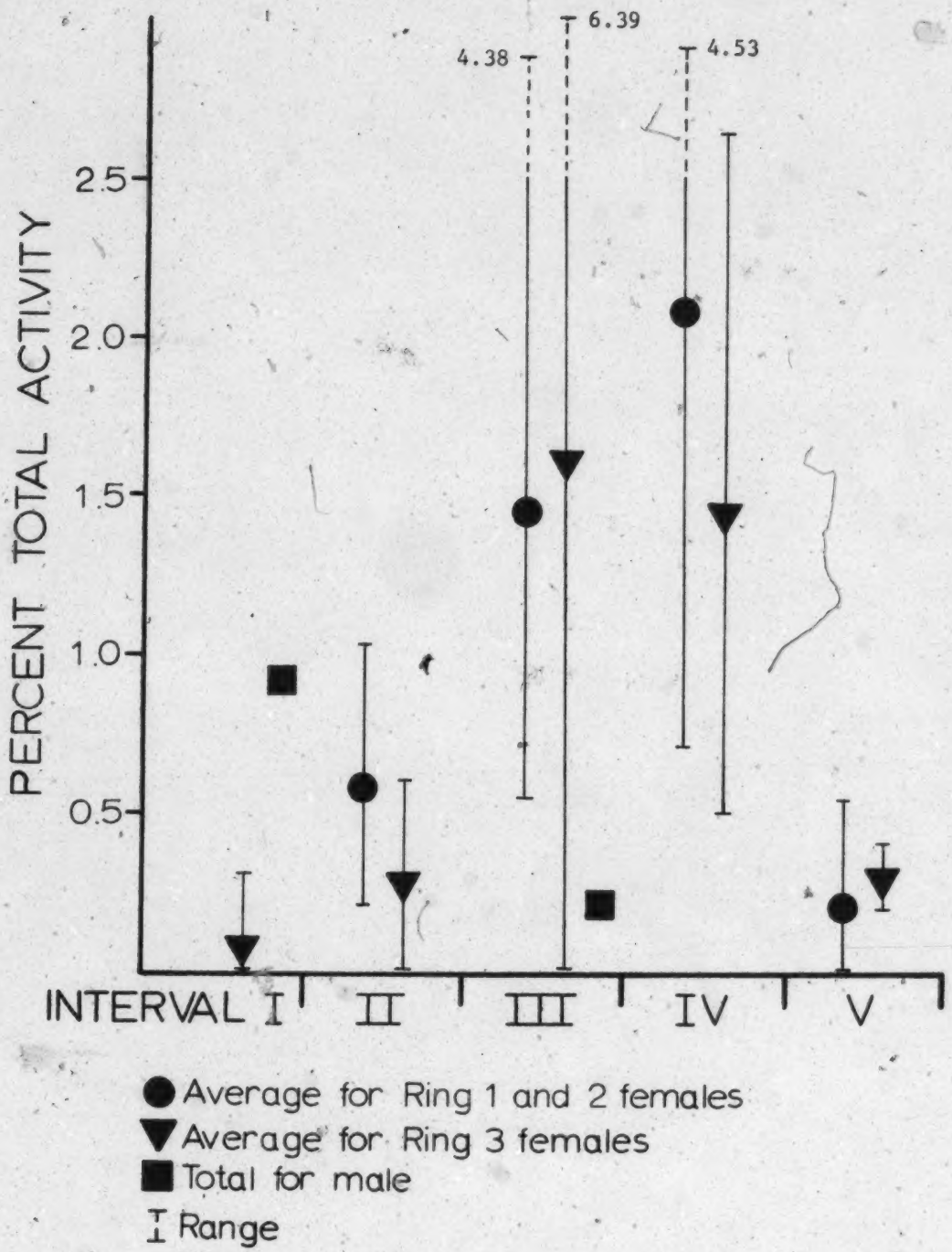

Figure 18: Investigating activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

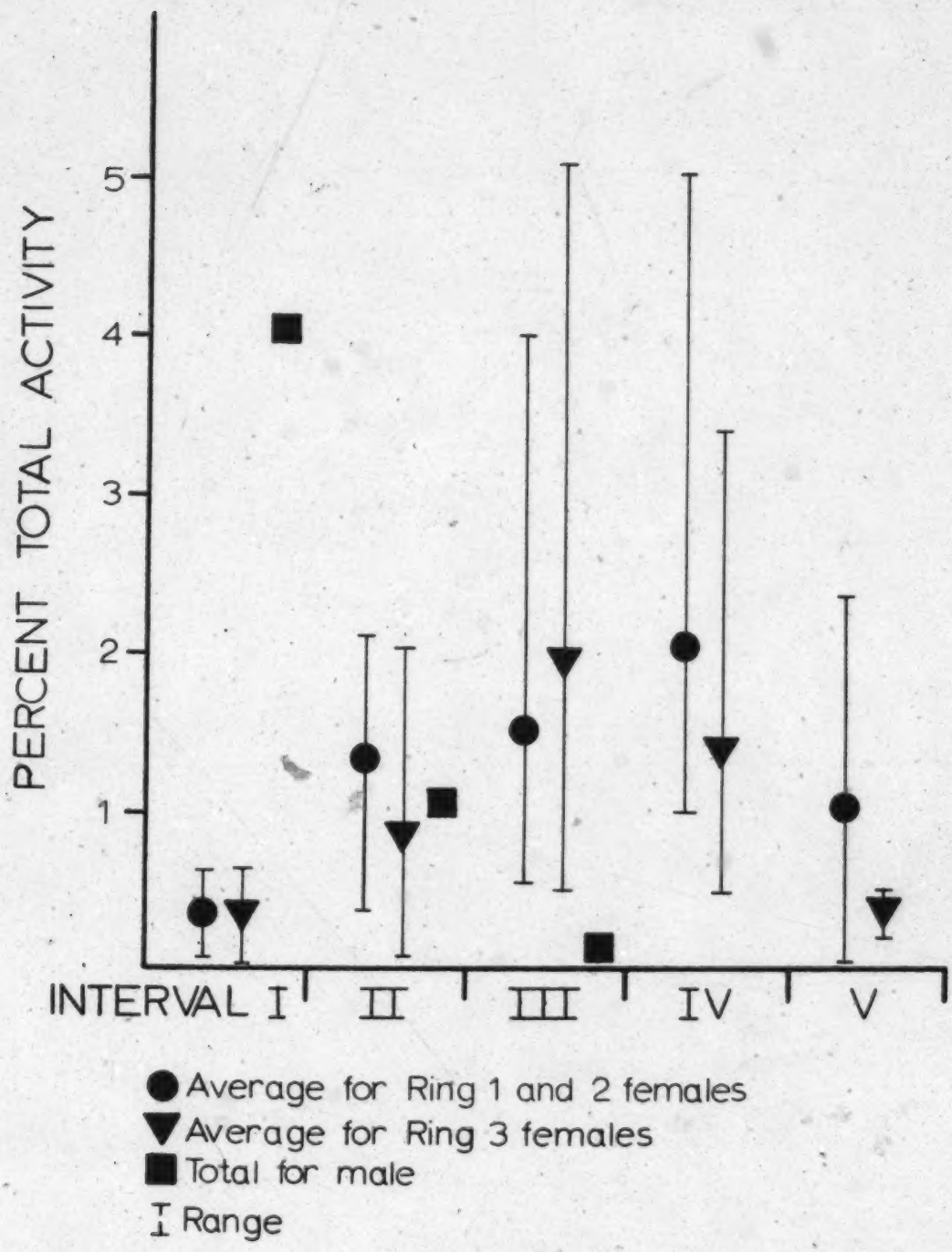

Figure 19: Visiting activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

Central females spent a larger percentage of time visiting than peripheral females during intervals II, IV, and V, while the average percentage of visiting was higher among peripheral females than central females during interval III. The differences between groups for intervals II and IV approach significance ($p=.20$). None of the other differences for the remaining groups were statistically significant.

The highest percentage of time spent visiting by any animal was recorded for the male during interval I. This activity would aid the male in locating sexually receptive females but visiting serves a broader function for all animals in the colony: by visiting, an animal familiarizes itself with burrow locations within as well as outside its own territory.

During interval I, the frequency of visits by all females was nearly equally divided between burrows within an animal's own territory and burrows elsewhere in the colony (Table 13). During intervals II, III, and IV, the increase in visiting activity by both groups of females was due to a large increase in the number of visits outside an animal's territory. Visiting by an animal within its own territory increased only slightly. For all three intervals that he was present, the male seldom visited burrows within his territory and almost all his visiting was done elsewhere in the colony.

During interval V, there was great variation in the relative frequency of visiting and no consistent difference was apparent between the two groups. The two ring 3 females remaining visited burrows within and without their own territories equally. Three of the five females remaining in ring 2 plus the central female (A) continued to visit outside their own territories more frequently than within them. The reverse was true

Table 13: Location of visits. Location of visits by each animal for each interval are given as actual frequencies. For statistical comparison, figures were converted to a percentage of the total amount of time each animal spent above ground.

	Interval	I		II		III		IV		V	
	Animal	H[1]	A[2]	H	A	H	A	H	A	H	A
R. 1	A	2	2	12	43	1	14	12	66	2	12
	B	3	2	4	41	8	13				
	C	4	3	0	11	1	6	6	20	0	0
	D	4	7	6	24	14	15	14	32	12	8
Ring 2	E	3	2	4	27	3	12	18	15	15	24
	F	1	1	1	42	0	21	8	39		
	G	2	0	12	29	12	12	18	13	5	9
	H	1	2	10	16	6	13	20	22	21	45
Total Ring 1 and 2		20	19	49	233	45	106	96	207	55	98
	I	5	3	5	6	7	21				
	J	0	4	2	5	1	15	7	14		
	K	2	5	1	32	0	7	0	14		
Ring 3	L	0	0	7	24	2	19	13	55	5	5
	N	0	0	0	3	2	5	3	4		
	O	0	2	3	20	5	10	8	10	4	4
	P	2	3	1	2	1	5	2	9		
Total Ring 3		9	17	19	92	18	82	33	106	9	9
	M	1	48	3	16	0	1				

[1] H= within own territory

[2] A= outside own territory

for the fourth female in ring 2 and the fifth female in ring 2 was not observed to visit at all before her disappearance early in the interval.

10. Marking. The percentage of time spent marking among females increased during the first few intervals of the season and decreased again at the end of the season (Figure 20). As with the occurrence of visiting, the percentage of time spent marking by peripheral females was greatest during interval III and was highest for central females during interval IV. Central females spent consistently more time marking than peripheral females for every interval. Differences between the two groups were slightly significant during interval I ($p<.10$) and significant for interval II ($p<.02$) and interval IV ($p<.01$). The highest incidence of marking by any animal was recorded for the male during interval I. After interval I, marking by the male declined, and for both intervals II and III, the incidence of marking by the male was lower than the averages for both central and peripheral female groups.

For both visiting and marking, the overall frequency increased from intervals I through IV although the overall density of animals in the colony was declining (Figure 21). Overall frequency was calculated as the frequency of each activity per animal present in the colony per hour of observation. Density of animals for each interval was an average of the maximum number of animals present above ground at one time for each day. There was no significant correlation between overall visiting frequency and density of animals or between marking frequency and population density.

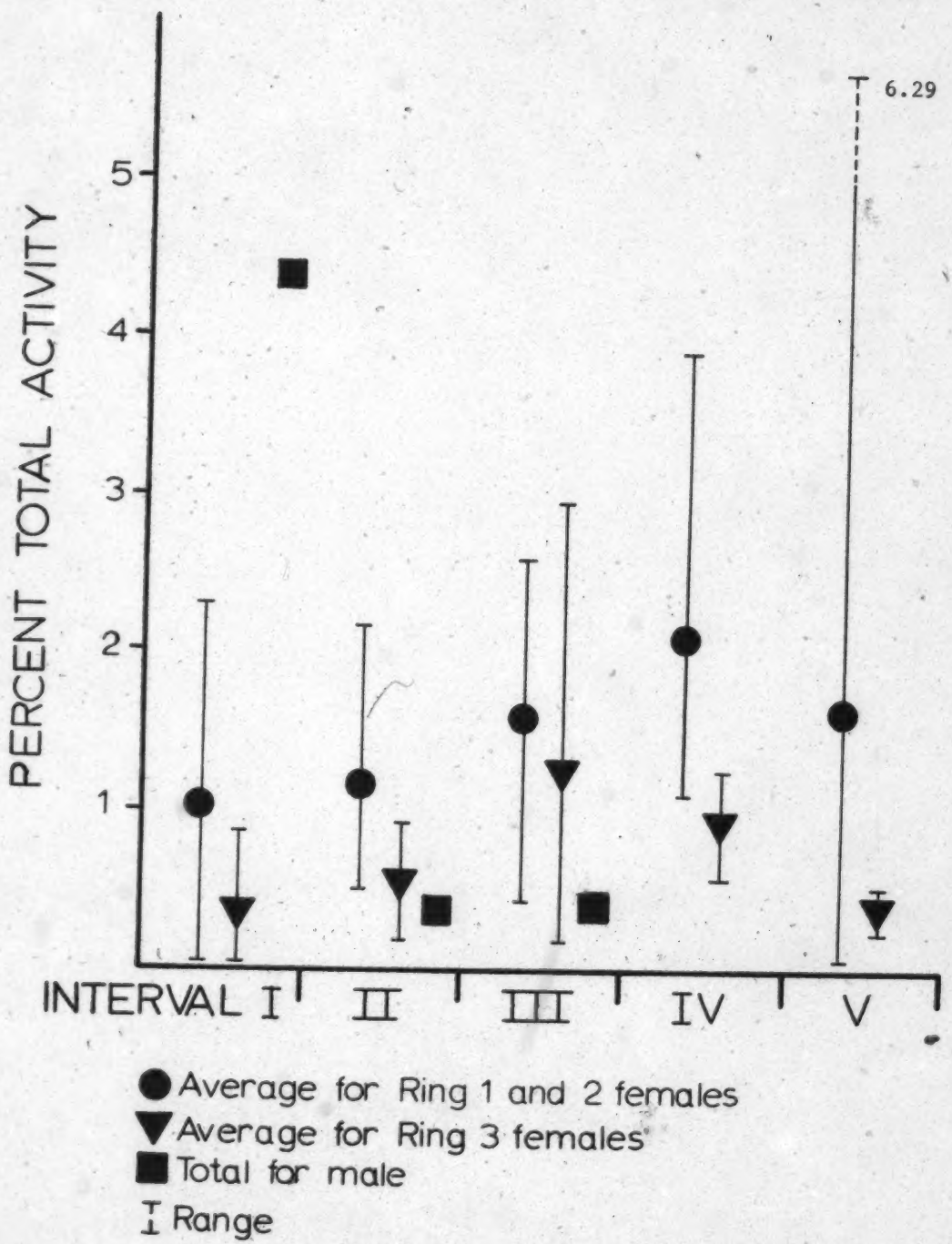

Figure 20: Marking activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

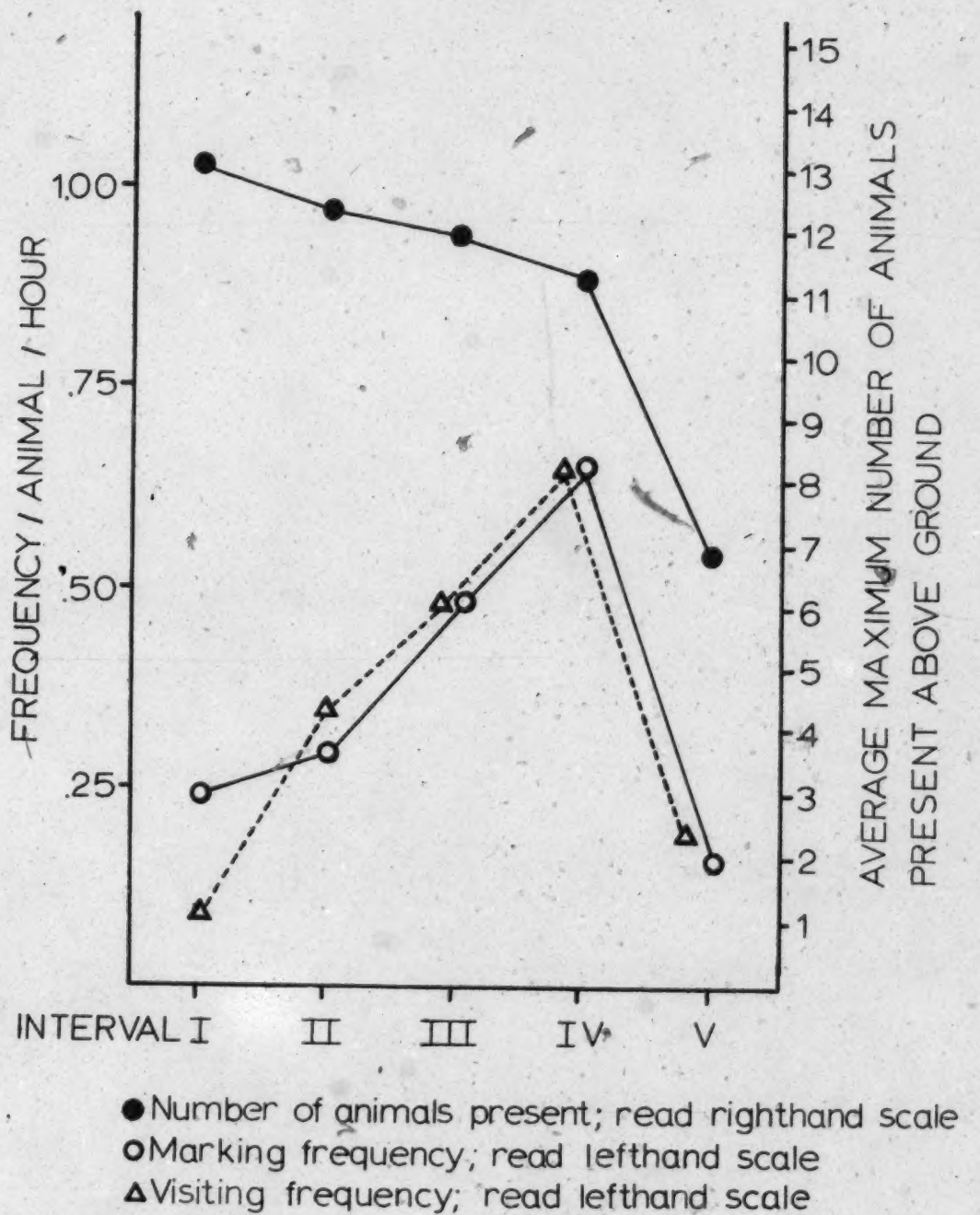

Figure 21: Marking and visiting frequency relative to population density of ground squirrels. Frequencies of marking and visiting by the male were omitted from the calculations.

11. Interacting. The amount of time spent interacting for both groups of females increased seasonally to a maximum during interval III and decreased during intervals IV and V to percentages lower than any of the preceding intervals (Figure 22). Central females interacted more than peripheral females during each interval. The differences between central and peripheral females were slightly significant during interval I ($p<.10$), significant for interval II ($p<.01$), and slightly significant during interval IV ($p=.10$). The percentage of time spent interacting by the male was considerably greater than that for both female groups during interval I, greater than peripheral females but less than central females during interval II, and less than both groups of females in interval III.

12. Activity differences between adult and yearling females. Of all eleven activities tested over all five intervals, there were only three activity differences between adults and yearlings that were slightly significant. During interval I, adults spent a greater percentage of time standing alert than did yearlings ($p=.10$). This greater wariness of the adults may be a reflection of longer experience. After interval I, this difference did not ocuur. During interval IV, adults had a higher percentage of visiting ($p=.10$) and interacting ($p<.10$) than did yearlings. The differences were probably due to the attempts of female K (AX3) to resettle near #29 following the death of female I. The change in location brought her into frequent encounters with female A(AL1) as well as female C(YX2). In addition female F still visited #27 although she no longer attempted to resettle there. This persistent trespassing caused frequent interactions between females F(AL2) and H(AL2) which

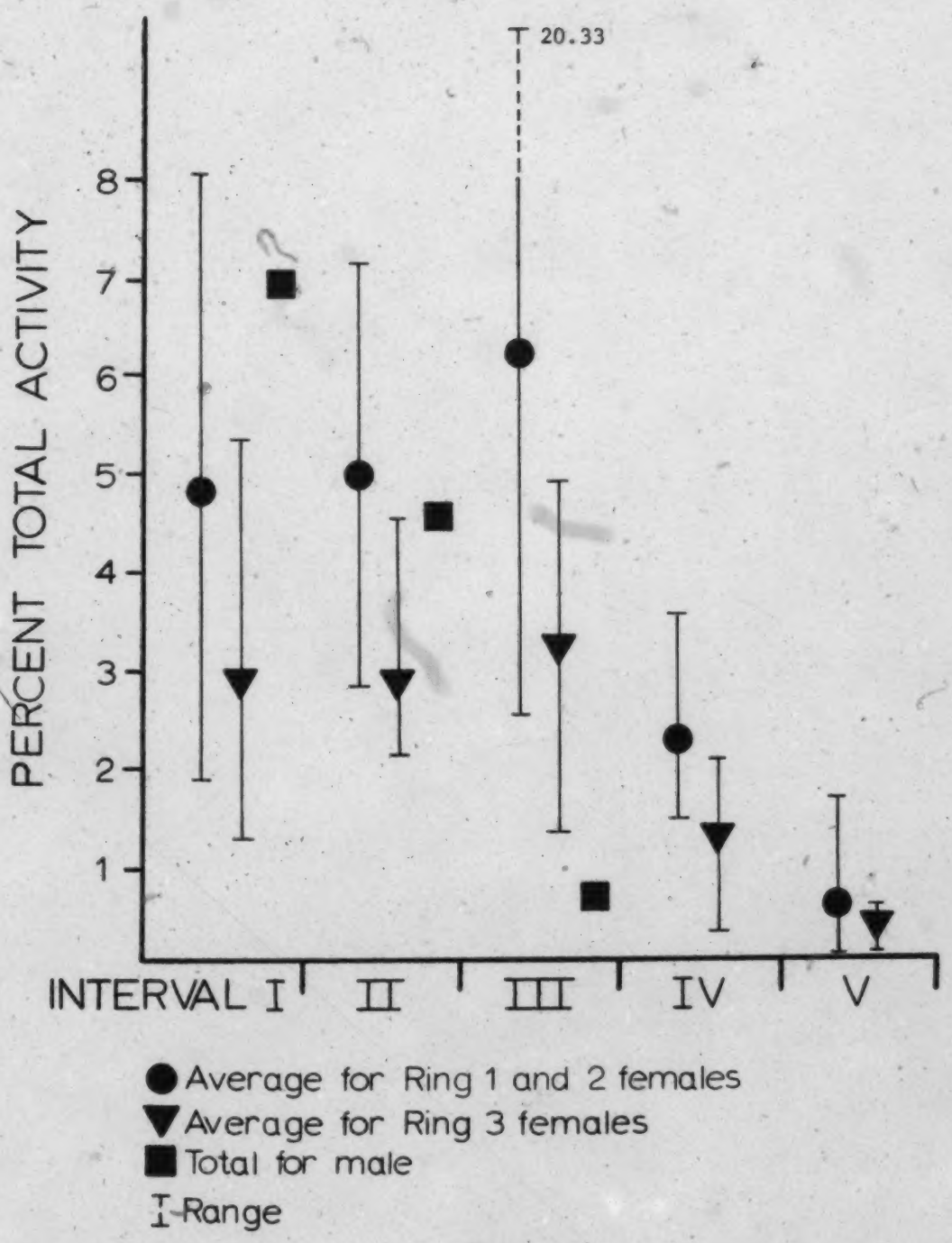

Figure 22: Interacting activity: Amount of activity expressed as a percentage of total time above ground for each animal for each interval. The range and average for both groups of females as well as the total for the male are illustrated for each interval. Sample size is the same as for figure 10.

contributed to the higher visiting and interacting scores of the adult females as a group.

SUMMARY OF ACTIVITY CHANGES AND DIFFERENCES BETWEEN FEMALE GROUPS

1. The highest occurrences of non-social behavior occurred during interval I (feeding, digging, sunning) or near the end of the season during intervals IV [sunning, grooming (peripheral female group)] and V [feeding, food gathering, grooming (central females)].

2. For all non-social activities, the only significant differences between groups was in bedding material collection. Central females (rings 1 and 2 combined) spent a consistently greater percentage of time at this activity, and differences between central and peripheral females were slightly significant for interval II and approached significance for interval III.

3. The highest percentages of social activity occurred during intervals III and IV. Marking, visiting, and investigating were highest for peripheral females during interval III and highest for central females during interval IV. The percentage of time spent interacting was maximum for both groups during interval III and the amount of alert behavior was maximum for both groups during interval IV.

4. The amount of alert behavior was consistently higher among peripheral females than central females for each interval but differences were not statistically significant.

5. There were no significant differences in investigating activity between central and peripheral females for any interval.

6. Central females spent more time visiting during intervals II, IV, and V than peripheral females but the differences only approached significance for intervals II and IV and were not significant for any other interval.

7. The occurrence of both marking and interacting was significantly higher for central females during intervals I, II, and IV.

8. There were only three slightly significant differences in activity between adult and yearling females.

DISCUSSION

The social organization of Richardson's ground squirrel in a parkland ecotone is a colony composed of nearly exclusive spatial territories with some evidence for a non-linear hierarchy superimposed on this system. Exclusive spatial territorial behavior is defined here as the defense of an area excluding all conspecifics, not only conspecifics of the same sex (Fisler, 1969). The only exception would be a brief period for breeding. Territorial boundaries are not permanently fixed in time and space but vary slightly during the season. Boundaries between territories are most clearly defined during the period following birth of the young but when young still remain underground. Following this interval, boundaries fluctuate as the result of agonistic encounters and become progressively less distinct. This is an organizational system based on individuals since there is no evidence for any sort of group co-operation except for group response to the alarm calls of individuals; there is no group co-operation in territory defence or burrow construction as mentioned by King (1955) for the prairie dog, *Cynomys ludovicianus*.

A definition of spatial organization based on the results of agonistic encounters (i.e. the exclusion of conspecifics) is preferable to the conventional definition of a "defended area" (Noble, 1939) since there is no evidence that the area itself is the object of aggressive behavior (Emlen, 1957; emphasis mine). Each female territory contained at least one nest site, but the territories could not be considered as nidic only since the area from which conspecifics were excluded included other major burrow systems besides the one containing the actual nest site. In addition, a territory was maintained by the one male in the colony as well

as by those females which did not raise litters.

The additional presence of a hierarchy is not incompatible with a system of territorial organization. "Hierarchies and territorial systems are not mutually exclusive concepts relating on the one hand to sociality and on the other hand to spatial utilization. Rather, these two concepts are actually the possible resultant extremes in the evolution of mammalian organizational systems with many possible intermediate types of systems employing various degrees of spatial territory and social hierarchy formation"(Fisler, 1969). Investigators have found hierarchies within territorial systems for the field mouse *Apodemus sylvaticus* (Brown, 1966), and for the house mouse *Mus musculus* (Crowcroft, 1955) and at high population densities a territorial species may shift to a hierarchical system. This has been reported for *Mus musculus* (Davis, 1958; Reimer and Petras, 1967) and for the chipmunk, *Tamias striatus* (Wolfe, 1966). Although in the last instance the high densities were created under laboratory conditions, it is reasonable to suppose that such a situation could develop within a free-living population as well.

That density may be a major factor in the social organization of my colony is demonstrated by comparing the population density of my study area with other populations of Richardson's ground squirrels. Yeaton's (1969) study area on the Saskatchewan prairie contained 1.18 to 3.26 females and 0.59 to 1.09 males per acre. Density for D. Michener's (1972) prairie population falls roughly within the same range as that of Yeaton's. Yeaton maintains that both sexes are territorial and does not mention any hierarchy among individuals. D. Michener stated that no hierarchy was evident for his population (pers. comm.). The only

investigator to report a ring arrangement of spatial organization with a dominant central female was Quanstrom (1968). Although his thesis reported only home ranges of females, the number of individuals on his study area indicates a density of 9.47 to 13.7 females per acre. In the present study, there were nine females and 0.56 males per acre. It would appear, then, that a hierarchy imposed on a system of territorial social organization occurs under conditions of high density. It is interesting to note that the higher population densities are due to an increase in the number of females in the population; there is little difference in the density of males on my area and that of Yeaton's.

Jewell (1966) defines home ranges as "the area over which an animal normally travels in pursuit of its routine activities." Results of the mobility index indicated that females spend from 20 to 50 percent of their time outside their territories and there is nothing to suggest that their activities during this time are anything but "routine". But when ring 1 and 2 females move outside their own territories, they are immediately trespassing on the defended area of another individual since territories are adjacent. A hierarchy allows a greater number of animals to occupy a given area than does a territorial system. I suggest that the population of ground squirrels on this study area was so dense that the home range of any one animal included the territories of several others and that the establishment of a hierarchy system served to decrease the antagonism that must invariably occur with such an overlap.

Home ranges for male Richardson's ground squirrels are consistently larger than those of females (Quanstrom, 1968; Yeaton, 1969). The nearly constant density of male *S. richardsonii* in spite of the variation in density of females may account for the very disproportionate male: female

ratio on my study area. It may be that while female *S. richardsonii* can adapt to high densities, males will not, and the study area is only large enough for one. This suggestion is supported by limited observations in 1973. This year two males were trapped on the study area in April. One had open wounds and fresh scars, the other was unmarked. By early May, only the unscarred male was present.

As Eisenberg (1966) suggests, "diurnal exploitation of open terrain could favor colony formation." A colonial aggregation of animals confers advantages on each individual. The presence of more than one animal multiplies the probability of detecting the approach of a potential enemy. It also provides a suitable social environment for successful mating and the rearing of young. The close proximity of the sexes in a colony would facilitate mating and since the male regularly moved over the entire study area it is unlikely that he would overlook a female in estrus. The breeding season occurs shortly after emergence from hibernation when climatic conditions limit the animal's above ground activity to only a few hours in the middle of the day and when little new grass is available. There would be little time or energy for males to seek mates very far distant. In addition, ground squirrels' reluctance to cross habitat barriers would limit the directions in which they could travel. All these limitations would serve to restrict breeding to the individuals within a colony. Young are protected in an underground nest for the first three or four weeks after birth and are later protected from other adults by remaining within their mother's territory after emerging above ground. The increased probability of predator detection afforded by a colonial group structure is advantageous to the young as well as to adult individuals. Also, the presence of numerous individuals

may sufficiently confuse a predator so that it would be less likely to notice individual minor burrow entrances to nest sites.

Some factor associated with social status and location may also influence reproductive success and this factor may exert more influence when population density is high. Although the number of females on the study area increased nearly 50 percent from 1971 to 1972, the number of young surviving to appear above ground was nearly equal. The average litter size was not smaller in 1972; instead, a smaller percentage of females were successful in raising a litter at all. The more dominant females were the more central females. The central female dominated females in rings 2 and 3; ring 2 females dominated their more peripheral neighbors in ring 3. Of the five females that did not raise litters, one lived in ring 2 and the other four in ring 3 (Appendix I). There were significantly more offspring raised in rings 1 and 2 than in ring 3 ($U=52.5$, $p<.05$). Location in relation to reproductive success has also been reported for marmots, *Marmota flaviventris* (Armitage, 1965). Fourteen of 19 litters over four years were concentrated in the central part of the colony, and in a sub-portion of a colony, only the central female raised a litter. Calhoun (1950) reported that subordinate rats had fewer litters. In a population of *S. tridecemlineatus*, McCarley (1970) found that 86 percent of ground squirrels in the population were decended from only 20 percent of the females present in 1963, but he does not mention location or social status of the females.

Transfer of live young from one nest to another was observed for six females on the study area and in several instances a litter was moved more than once. There was no consistent trend in the direction of litter transfer and this activity was not exclusive to either

dominant or subordinate females. However, litter transfer may serve to decrease the probability of olfactory detection by a predator if nests were vacated after they had been fouled by young ground squirrels over a period of days or weeks. Evans and Holdenried (1943) reported the transfer of young *S. beechyii* by their mother and on investigating found a rattlesnake at the old nest site.

The incidence of food gathering was highest for each group of animals on the study area during the interval just prior to their entrance into torpor. For the male, this was interval II, for peripheral females intervals IV and V, and interval V for central females. The high incidence of food gathering is likely related to the increase in amount of time spent feeding prior to the animal's disappearance. Stored food would allow the animal to feed during inclement weather or after dark to facilitate maximum weight gain before torpor. However, the possibility of some of this food, especially seeds, remaining uneaten long enough to serve as an emergency food source during or shortly after hibernation remains to be investigated. Since no burrow systems were excavated during this study, the possibility of stored food remains only a suggestion. The irregular occurrence of food piles separate from bedding material has been reported for *S. undulatus* (Krog, 1954), *S. lateralis* (Gordon, 1943), *S. beecheyii* (Fitch, 1948), and *S. columbianus* (Shaw, 1926).

Non-injurious types of agonistic encounters comprised a greater portion of interactions as the season progressed. A stable social organization should serve to reduce conflict among the individual members. The highest incidences of potentially injurious encounters occurred when the social organization was least stable, i.e. during interval I when animals were establishing territories initially and during interval III

when some peripheral females were attempting to resettle in a more central location. Among chipmunks (*Tamias striatus*), chasing and fighting declined after the establishment of territories (Wolfe, 1966) and in round-tailed ground squirrels (*S. tereticaudus*), fighting occurred most often when squirrels were attempting to establish residency (Drabek, 1970). The most frequent component of interactions among *S. richardsonii* was chasing and the same has been reported for the tree squirrel, *Tamiasciurus* (Smith, 1968), and the golden-mantled ground squirrel, *S. lateralis* (Wirtz, 1967).

The components of interactions varied according to the animals' age class and location. There were consistently more interactions between neighbors than between non-neighbors which is consistent with the establishment and maintenance of territorial boundaries between adjacent animals. Both the most severe and the least severe components of agonistic encounters were more frequent between neighbors than between non-neighbors. This may be related to recognition of and pressure on established boundaries respectively. Chases were most frequent between non-neighbors. A non-neighboring trespasser may be less aggressive due to greater distance from her own territory, and unfamiliarity with territorial boundaries beyond her own and her neighbors' so that fewer contact encounters (fighting, attacking) between non-neighbors would result. Among marmots, most agonistic behavior occurs between neighbors (Armitage, 1965). The difference in frequency and severity of encounters among yearlings as compared to adults and between adults and yearlings probably reflects the greater lack of social experience of the younger animals. Among marmots, the number of interactions between adults and yearlings increased for the first three weeks following emergence and then the frequency and severity declined for the remainder of the season (Armitage, 1965).

One advantage of colonial organization is that the combined watchfulness of its members increases the probability of early detection of a predator. Although the differences were not statistically significant, peripheral females consistently spent more time standing alert than central females, except during the interval that the weasel resided near the center of the ground squirrel colony. All hawks approached the colony flying very low, rather than dropping directly from higher altitudes, and all ground predators had to first cross the peripheral areas to reach the central ones. Therefore it is reasonable that peripheral animals, having fewer neighbors than central animals, would benefit from longer and more frequent periods of alert behavior; this would also be beneficial for other members of the colony. What actually motivates peripheral animals to spend a greater amount of time in alert behavior is not apparent. Support for a relationship between alert behavior and predator detection is provided by the relative amounts of alert behavior during interval IV when the weasel resided in the central portion of the colony. During this interval only, central females showed a higher percentage of alert behavior than peripheral animals. The high amount of watchfulness by the male is consistent with his peripheral position but the percentages are so much higher than either group of females that there may be an additional explanation for his vigilance. It has already been mentioned that male Richardson's ground squirrels do not exist together at the same high densities as do females, and alert behavior would aid in the detection of other ground squirrels as well as predators. If the reduced density of males is a reflection of a greater intolerance for conspecifics of the same sex, then perhaps this heightened degree of intolerance also stimulates a heightened degree of watchfulness among

male ground squirrels. There was another ground squirrel colony 200 meters distant on the far side of the marsh. This colony contained one male and the movements of the animals were visible from the study area. Perhaps the presence of another male 200 meters away is sufficient to stimulate increased watchfulness in another resident male. Another possibility is that the male may be less tolerant of conspecifics from outside the colony, irrespective of the sex of the trespasser. Strange ground squirrels entered the colony infrequently and were immediately vigorously pursued by a number of residents which almost always included the male, irrespective of the location of the trespasser. Since strangers were driven out of the colony so rapidly, it was not possible to trap them to determine their sex.

Marking behavior has been described for several species of ground squirrels. Wirtz (1967) describes what appears to be marking behavior for *S. lateralis*, but calls it a type of displacement behavior associated with agonistic encounters, and Drabek (1970) expressed the possibility of scent marking for *S. tereticaudus*. Adult male *S. beecheyii* mark frequently in the vicinity of their home burrows, and marking is even more noticeable in those exploring nearby burrow systems (Fitch, 1948). Among arctic ground squirrels (*S. undulatus*) in enclosures, males "rub" more than females, but this marking is not a deterrent to territorial invasion (Watton, 1969). Among *S. richardsonii*, Quanstrom (1968) reported the dominant female rubbing the area just posterior to her ear on her own burrow hill and on the burrow mounds of other squirrels. Among all reports of marking in mammals, Richardson's ground squirrel is unique in that except for interval I, marking is done predominantly by females. The male spent considerably more time marking than both groups of

females during interval I, but after this interval, he marked less than most of the females on the area. In marmosets, *Callithrix jacchus*, Epple (1970) found that marking frequency of the dominant male increased in the presence of a strange male or following exposure to the scent of a strange male. In rabbits, *Oryctolagus cuniculus*, the chin glands used in marking are larger in males than in females and the glands are largest and most active during the breeding season (Mykytowycz, 1965). Therefore, the decrease in marking by the one male may have been due to the absence of other males in the colony. But if marking frequency is related to reproductive condition, then marking frequency might decline after the breeding season irrespective of the presence of other males.

Among the two groups of females, interacting and marking were the only activities that were significantly different between dominant and subordinate females. Females in ring 2 spent more time marking than females around the periphery and the centralmost female marked one and one half times more frequently than any female in ring 2. All animals marked in the vicinity of their own burrows as well as on or near the burrows of other individuals. Marking is apparently no deterrent to territorial invasion in this species since trespassing occurred frequently, irrespective of the frequency of marking in various areas. Between central and peripheral females, there was no significant difference in the amount of time spent visiting, yet the amount of time spent marking outside an individual's territory was greater for central females. Since visiting and marking behavior frequently occurred sequentially, it follows that although all animals had nearly the same opportunity to leave a scent as they moved about the area, central females did so to a much greater extent than peripheral females. Epple (1970) found that

dominant female marmosets mark more frequently than subordinate females and the marking frequency of the dominant female increases in response to the presence or the scent of a strange female. Ralls (1971) maintains that "the species which have been studied experimentally tend to mark frequently in any situation where they are both intolerant of and dominant to other members of the same species. Such behavior will occur in territorial defense but is by no means restricted to territorial situations." The degree of intolerance between female *S. richardsonii* has not been considered, and marking among these animals is not restricted to within individual territories nor does it inhibit trespassing. Although the message conveyed by marking is not understood, there is a definite positive relationship between high frequency of marking and relative dominance within a group of female Richardson's ground squirrels.

Differences in percentage time spent feeding, digging, grooming, and sunning were not significant between central and peripheral females for any interval. The high incidence of feeding following emergence from hibernation and again just prior to entrance into torpor is probably related to the energy requirements of hibernation. Sunning activity appears related to low temperature and inclement weather. Digging activity is more frequent at the beginning of the season when existing burrow systems are in a state of disrepair. The greater percentage of digging activity among peripheral females was undoubtedly due to the fact that there was an overall increase in population size from 1971 to 1972 and there were fewer existing burrow systems around the periphery where the additional animals settled. Both digging and feeding activities have implications for overwinter survival for the individual, but are not directly related to the individual's social position within the group.

The percentage of grooming, more than any other non-social activity seemed to change inversely with the amount of time spent in various social activities. This is quite plausible since all activities were compared as percentages of an animal's total time above ground. Thus the less time spent on social activities was reflected in an increase most noticeably in grooming, a non-social activity.

Most of the non-social activity differences were not statistically significant due to the wide range of individual variation within each group of females. To test for other factors that might cause this variability within each group, additional tests were made comparing percentages of activities between adult and yearling females and between lactating and non-lactating females. The few differences between adult and yearling females were only slightly significant. Since more lactating females lived in the central rings and most non-lactating females were located around the periphery, these group comparisons could not be considered independent of ring position. However, the only significant differences were in marking and interacting, and as such, probably reflect differences in social status rather than reproductive condition. One last comparison was made to try and explain the variation within central and peripheral groups. The eight hours of observation each day were divided into four two-hour intervals and the activities of each group were compared within each interval for each activity to determine any temporal difference in activity occurrence or duration. The infrequent significant differences corresponded to the activity comparisons between groups for entire days; percentage of time of various social activities (i.e. marking, interacting) was higher for central than peripheral females

with no difference in the temporal occurrence of any activity. The wide range of individual variation within each group of females remains unexplained.

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APPENDIX I

Number of offspring surviving to appear above ground for each female ground squirrel in 1972.

	Female	Age Class	Number of Offspring
R. 1	A	A	5
Ring 2	B	Y	7
	C	Y	0
	D	Y	6
	E	Y	7
	F	A	2
	G	Y	5
	H	A	7
Ring 3	I	A	5
	J	Y	0
	K	A	0
	L	A	2
	N	A	0
	O	Y	5
	P	U	0
	Q	U	4

A = adult

Y = yearling

U = age class unknown

APPENDIX II

Since animals were above ground for various amounts of time during each interval, the amount of time spent on each activity by each individual animal was expressed as a percentage of the total time the animal was recorded above ground. In some cases, the percentages total slightly less than 100 percent since some miscellaneous activities occurred too infrequently to be used in a statistical comparison. These miscellaneous activities included time spent chasing the weasel, allo-grooming, and interactions between females and their offspring such as playing and grooming. Play was not observed between adult ground squirrels. Actual time spent above ground and percentage of time spent on each activity are given for each of 16 animals for each interval. Very few observations were recorded for female Q until she moved to burrow #29 during interval IV. Data for this animal are not included in the appendix and were not used in any statistical analyses.

*Although the underlying assumption is that the amount of variation between each ring was correlated with social status, occasionally other variables also contributed slightly to the variation.

Appendix II (continued)

Interval I, April 17 to May 7

Animal	Total time above ground (minutes)	Feeding	Digging	Visiting	Marking	Grooming	Alert	Interacting	Bedding material collection	Investigating	Food gathering	Sunning
A	1457	79.82	6.52	.27	.96	.96	1.17	5.63	4.32			.34
B	1323	68.48	19.05	.53	1.36	.91	1.97	2.80	5.67			
C	1837	62.55	14.32	.38	2.29	3.76	3.05	6.80	5.39			1.47
D	1634	59.49	9.73	.67	1.77	2.75	2.57	8.08	14.75			.18
E	1326	83.71	1.66	.38	1.21	1.89	4.37	5.96	.38			.45
F	1603	61.95	24.02	.12	.50	2.18	4.12	3.99	2.06			1.06
G	1368	63.52	24.12	.15	.15	1.68	1.24	3.80	5.34			
H	1345	80.30	10.41	.22		1.49	5.65	1.93				
I	1590	70.19	9.12	.50	.88	.75	7.86	3.52	7.04			.13
J	1017	68.53	24.39	.39	.39	.30	2.95	2.16	.59			.30
K	1344	61.31	16.67	.52	.15	5.88	4.54	5.36	4.32	.30		.97
L	1081	50.14	33.86		.28	2.68	2.87	3.52	6.01			.65
N	803	48.69	27.77		.50	1.49	12.70	2.12	6.72			
O	301	94.68		.66			1.99	2.66				
P	1457	80.30	9.06	.34	.14	3.09	4.05	1.24	.69			1.10
M	1219	58.82	4.84	4.02	4.35	3.86	12.88	6.97		.90		3.36

Appendix II (continued)

Interval II, May 8 to May 30

Animal	Total time above ground (minutes)	Feeding	Digging	Visiting	Marking	Grooming	Alert	Interacting	Bedding material collection	Investigating	Food gathering	Sunning
A	3067	58.46	18.13	1.79	1.11	1.73	4.43	7.21	5.45	1.14		
B	2649	62.36	12.72	1.70	2.15	2.57	7.55	5.21	4.91	.68		
C	3072	54.10	24.02	.36	1.50	6.02	30.50	4.43	8.04	.46	.03	.16
D	2639	67.68	3.98	1.06	1.25	.38	5.19	5.19	13.26	.19	.30	
E	2434	67.91	6.20	1.27	.70	1.48	6.16	4.68	11.26	.25	.04	
F	1966	70.09	7.63	2.19	1.12	1.73	5.39	6.51	4.07	1.02	.05	.20
G	3084	62.52	19.29	1.33	.91	1.91	5.35	3.73	3.57	.68	.10	
H	2711	73.77	14.16	.96	.48	1.44	3.43	2.88	2.07	.26	.52	
I	2507	77.38	5.15	.44	.40	1.28	4.99	3.39	4.87	.20	.04	
J	2009	79.09	6.22	.35	.40	2.19	8.86	2.14	.45	.30		
K	2201	55.75	11.49	1.50	.91	4.82	16.31	4.59	4.36	.27		
L	1530	52.09	33.14	2.03	.20	.72	7.97	3.14	.33	.33	.07	
N	1476	49.86	22.97	.20	.54	5.42	15.85	2.57	1.63	.61		.34
O	1925	75.53	6.91	1.19	.83	.52	8.62	2.44	1.61	.26	.47	
P	2809	66.75	6.55	.11	.64	9.04	4.73	2.14	7.33			.11
M	1739	62.16	4.54	1.09	.35	7.02	13.57	4.60	2.99		.40	3.28

Appendix II (continued)

Interval III, June 1 to June 14

Animal	Total time above ground (minutes)	Feeding	Digging	Visiting	Marking	Grooming	Alert	Interacting	Bedding material collection	Investigating	Food gathering	Sunning
A	1368	34.92	21.18	.92	1.77	2.32	8.91	4.64	7.27	.98	.18	
B	1097	67.91	2.83	1.73	2.10	.73	16.41	20.33	.73	1.82	.46	
C	1175	57.19	.34	.60	1.79	5.87	6.47	4.60	21.53	.94	.17	
D	1083	57.18	19.47	1.55	1.83	1.05	7.38	4.33	3.99	.67	.67	
E	1445	56.33	19.79	1.04	.42	1.25	10.45	3.05	5.47	.76	.07	
F	525	70.10	1.14	4.00	1.71	1.52	8.00	7.81	2.86	4.38		
G	1884	55.52	20.86	1.27	2.55	5.47	8.33	2.71	.37	.53	.11	.32
H	1418	54.58	12.62	1.34	1.34	1.27	10.01	2.61	12.34	1.55	.92	
I	1278	59.23	18.54	2.19	.86	1.56	9.31	4.93	1.88	.23	.16	
J	755	74.04		2.12	1.06	3.31	9.40	4.90	1.06	.93	.13	
K	487	69.20		1.44	.21	4.31	12.94	4.11	6.16	1.03		
L	407	64.86		5.16	2.95	5.16	8.60	3.19		6.39		
N	511	67.51	4.11	1.37	1.96	1.57	14.48	2.94	2.15	2.54		
O	1289	48.49	28.39	1.01	1.01	2.95	12.88	2.25	1.63		.16	
P	1178	56.79	17.49	.51	.68	10.36	10.36	1.36	2.04	.25	.08	
M	540	77.22	1.30	.19	.37	4.26	15.00	.74	.74	.19		

Appendix II (continued)

Interval IV, June 15 to June 30

Animal	Total time above ground (minutes)	Feeding	Digging	Visiting	Marking	Grooming	Alert	Interacting	Bedding material collection	Investigating	Food gathering	Sunning
A	2913	61.52	.17	2.64	3.91	3.81	17.03	3.64	.41	4.53	.07	.14
B	killed June 14											
C	2262	75.33	.18	1.11	1.81	3.23	12.73	1.59	.80	1.24	.35	
D	2871	76.52	.80	1.60	1.95	2.02	11.32	1.81	.07	1.18	.38	
E	2822	72.22	1.95	1.17	1.67	2.30	14.21	1.74	.07	.71		
F	934	51.61		5.03	2.68	1.18	27.94	3.21		4.07		
G	3136	69.77	2.07	.99	1.08	4.37	11.67	1.82	.96	1.28		3.57
H	2441	55.29	9.79	1.74	1.66	5.06	15.64	2.49	5.39	1.62		
I	killed June 14											
J	1790	87.71	1.17	.56	.67	6.26	.78	.34	.89	.45		
K	977	69.09	.31	1.43	.82	8.29	12.90	2.05	.31	2.66	.10	1.33
L	2010	67.21	1.19	3.38	1.24	4.43	11.14	1.89	4.58	2.39	.10	
N	1399	79.70	4.57	.50	.93	2.64	9.08	.36	.79	.50	.14	.50
O	2250	65.33	.93	.80	.98	4.62	20.17	1.56	1.91	1.02	.09	
P	969	72.45	.41	1.14	1.14	7.12	11.66	1.34	2.89	1.03	.41	
M	last observed June 5											

Appendix II (continued)

Interval V, July 1 to July 30

Animal	Total time above ground (minutes)	Feeding	Digging	Visiting	Marking	Grooming	Alert	Interacting	Bedding material collection	Investigating	Food gathering	Sunning
A	2846	84.65		.49	1.30	4.46	5.20	.70	.49	.56	.18	
B												
C	334	67.66			6.29	22.46	.60	1.80			.60	
D	859	84.87		2.33	.81	4.54	4.54	.58	.70	.23	.93	
E	2972	84.83	.03	1.31	.74	1.99	8.24	.07	.37	.07	.37	
F	moved off study area June 29											
G	1696	87.97	.18	.83	.06	1.89	5.54	.53	.88	.12		.41
H	5282	81.69	.11	1.25	.68	2.46	11.17	.32	.04	.32	.06	.06
I												
J	last observed June 30											
K	last observed June 30											
L	2181	83.95	.28	.46	.37	3.35	8.76	.46	.32	.37		.18
N	last observed July 4											
O	2318	84.17	.26	.35	.47	1.77	11.22	.35	.35	.22	.56	
P	last observed June 27											
M												